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BIBLIOGRAPHIC DATA SHEET

1. Report No. APTD-0759

2.

3. Recipient's Accession No.

4. Title and Subtitle AICE Survey of USSR Air Pollution Literature - Volume IX - Gas Resistance of Plants With Special Reference to Plant Biochemistry and to the Effects of Mineral Nutrition

5. Report Date January 1971

6.

7. Author(s) M. Y. Nuttonson

8. Performing Organization Rept. No.

9. Performing Organization Name and Address
American Institute of Crop Ecology
809 Dale Drive
Silver Spring, Maryland 20910

10. Project/Task/Work Unit No.

11. Contract/Grant No. 1
R01 AP00786-APC

12. Sponsoring Organization Name and Address
Environmental Protection Agency
Air Pollution Control Office
Research Triangle Park, North Carolina 27711

13. Type of Report & Period Covered
the following:

14.

15. Supplementary Notes DISCLAIMER - This report was furnished to the Office of Air Programs by American Institute of Crop Ecology, 809 Dale Drive, Silver Spring, Maryland 20910 in fulfillment of Grant 1 R01 AP00786-APC

16. Abstracts

A collection of eight selected reports on air pollution investigations conducted in USSR, are presented. The reports deal with ~~(1)~~ an extensive survey of the principal advances in research on the gas resistance of plants and of the causes of plant vulnerability to gas; and ~~(2)~~ a number of investigations conducted in laboratories and on field plots of the Botanical GArden of Perm University ~~(a)~~ in reference to the feasibility of regulating the gas resistance of plants by means of certain nutritional elements, ~~(b)~~ in reference to a number of biochemical and physiological indicators that can be used to solve the problem of diagnostics of the gas resistance of plants and to characterize species differences in their gas resistance, and ~~(c)~~ to determine the minimum-permissible norms of certain air pollutants for individual species of plants.

17. Key Words and Document Analysis. 17a. Descriptors

Air pollution	Minerals
Plants (botany)	Plant metabolism
Forage grasses	Carbon 14
Resistance	Sulfur dioxide
Exhaust gases	Plant pigments
Dust	Plant chemistry
Nutrition	Plant nutrition

17b. Identifiers/Open-Ended Terms
Air pollution effects (plants)
USSR
Biochemoluminescence

Details of illustrations in this document may be better studied on microfiche

17c. COSATI Field/Group 13B, 6C

18. Availability Statement Unlimited

19. Security Class (This Report) UNCLASSIFIED

20. Security Class (This Page) UNCLASSIFIED

21. No. of Pages 123

22. Price

AICE* SURVEY OF USSR AIR POLLUTION LITERATURE

Volume IX

GAS RESISTANCE OF PLANTS WITH SPECIAL REFERENCE TO PLANT BIOCHEMISTRY AND TO THE EFFECTS OF MINERAL NUTRITION

Edited By

M. Y. Nuttonson

The material presented here is part of a survey of
USSR literature on air pollution
conducted by the Air Pollution Section
AMERICAN INSTITUTE OF CROP ECOLOGY

This survey is being conducted under GRANT 1 RO1 AP00786 – APC
AIR POLUTION CONTROL OFFICE
of the
ENVIRONMENTAL PROTECTION AGENCY

*AMERICAN INSTITUTE OF CROP ECOLOGY
809 DALE DRIVE
SILVER SPRING, MARYLAND 20910

1971

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PREFACE

In the USSR, the rapid development of various industrial enterprises and the extensive use of the internal combustion engine for motor vehicle transportation contribute greatly to massive qualitative changes in the habitat of living organisms through an ever increasing pollution of air, soil, and streams. In many industrial areas and in large cities new environmental conditions are being created which can sustain the existence of no plant life at all or only of the most pollution-resistant plant species or some of its variant forms.

The resistance of plants to pollution varies with a whole complex of factors, primarily with type of emission, growth conditions, the physiological-biochemical and morphological characteristics of a given plant species, the developmental stage of the plants, and the nature of the exposure. The combination of these factors appears to govern to a large degree the resistance of a plant species, as well as of its ecotypes, and its varieties or cultivars.

For plant scientists, two approaches are available to counteract the noxious effects of pollution, namely:

(a) One approach rests on the recognition that plant species differ in their resistance to a given pollutant or to certain combinations of pollutants, and also that differences in resistance to pollution have been found to exist in individual plants or varieties within certain species. It should be possible, therefore, to obtain by selection plants resistant to certain pollutants and thus suitable to areas where such pollutants prevail. It is self-evident that in the assessment of environmental conditions prevailing in a given area the nature of air pollution must be considered in relation to all the other potent physical and biological stresses and factors governing the overall problem of plant selection and plant adaptation.

(b) The second approach rests on the observation that certain agrotechnical field practices, notably a judicious supply of mineral nutrients, increase the resistance of plants to air pollution.

The present volume consists largely of reports dealing with (1) an extensive survey of the principal advances in research on the gas resistance of plants and of the causes of plant vulnerability to gas, and (2) a number of investigations conducted in laboratories and on field plots of the Botanical Garden of Perm' University (a) in reference to the feasibility of regulating the gas resistance of plants by means of certain nutritional elements,

(b) in reference to a number of biochemical and physiological indicators that can be used to solve the problem of diagnostics of the gas resistance of plants and to characterize species differences in their gas resistance, and (c) to determine the minimum-permissible norms of certain air pollutants for individual species of plants.

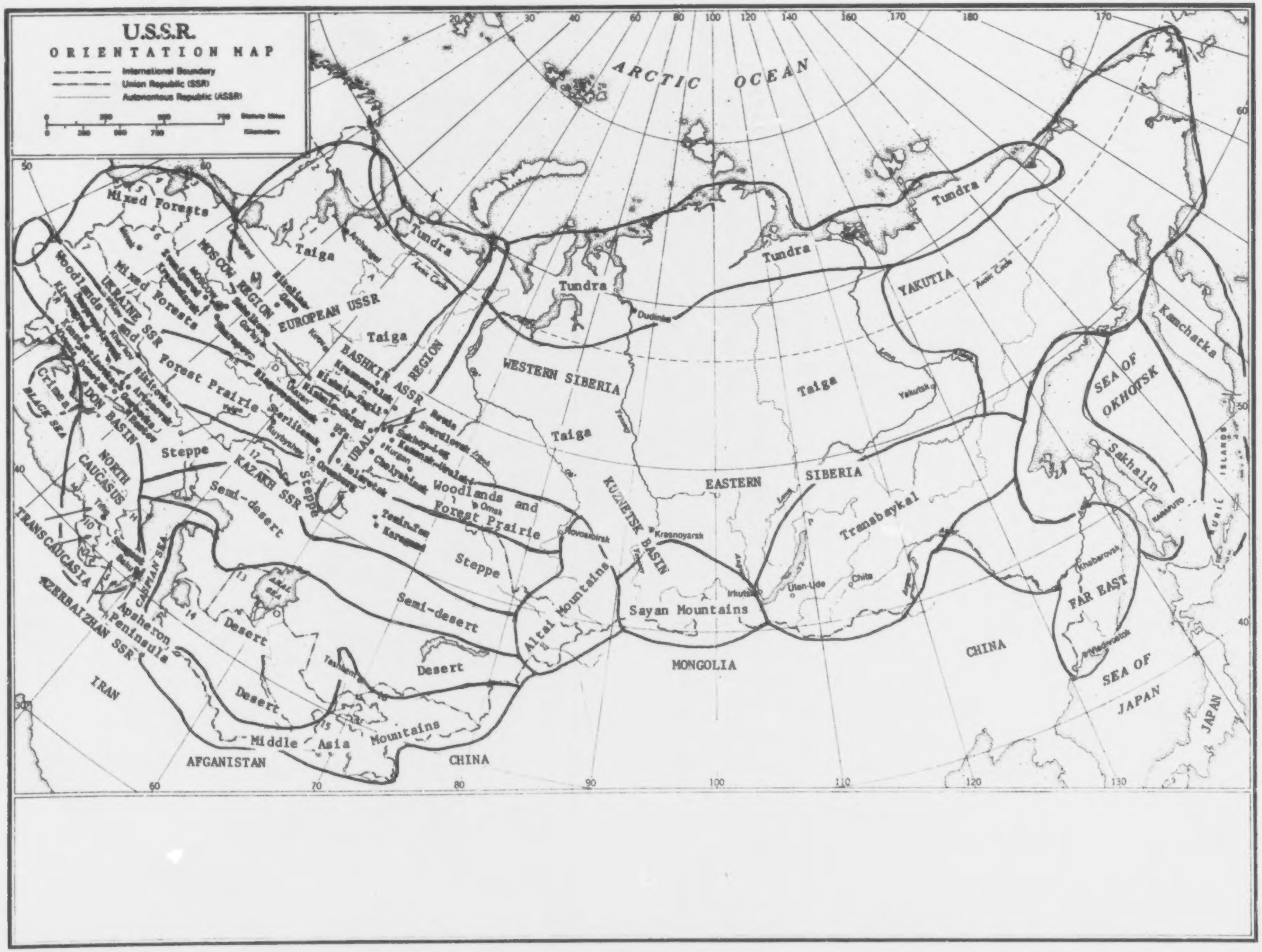
Perm', where these investigations were conducted, is an area lying in the highly industrialized Ural Region, which occupies a most important position in the industrial economy of the USSR. The local vegetation of Perm' and its environs, as well as that of the whole industrialized Ural Region and that of a great many other highly industrialized areas and regions of the USSR is badly affected by the increasing contamination of the natural environment with the toxic emissions from numerous industrial enterprises and power plants.

Some background information on the distribution of the Soviet industry's production machine may be of interest in connection with that country's present and potential pollution problems and investigations. The planned distribution of production in the Soviet Union favors effective exploitation of the natural resources of the USSR, especially in its eastern areas where enormous natural resources are concentrated, and has led to the creation of large industrial centers and complexes of heavy industry in many of the country's economic areas (see page ix). The many diverse climatic conditions of the country and its major economic areas as well as the geographical distribution of the Soviet Union's principal industrial and mining centers and of its principal electric power stations and power systems can be seen from the various maps presented as background material in this volume.

It is hoped that the selected papers will be conducive to a better appreciation of some of the air pollution investigations conducted in the USSR. As the editor of this volume I wish to thank my co-workers in the Air Pollution Section of the Institute for their valuable assistance.

M. Y. Nuttonson

September 1971


U.S.S.R.
ORIENTATION MAP
International Boundary
Union Republic (SSR)
Autonomous Republic (ASSR)
Statute Miles
Kilometers
ARCTIC OCEAN
Tundra
Taiga
Mixed Forests
MOSCOW REGION
EUROPEAN USSR
UKRAINE SSR
Woodlands and Forest Prairie
Forest Prairie
Steppe
Crimea
BLACK SEA
DON BASIN
NORTH CAUCASUS
TRANSCAUCASIA
AZERBAIZHAN SSR
Apsheron Peninsula
CASPIAN SEA
IRAN
AFGANISTAN
Middle Asia Mountains
Desert
Semi-desert
KAZAKH SSR
BASHKIR ASSR
URAL REGION
WESTERN SIBERIA
Woodlands and Forest Prairie
KUZNETSK BASIN
Altai Mountains
Sayan Mountains
MONGOLIA
CHINA
EASTERN SIBERIA
Transbaykal
YAKUTIA
FAR EAST
SEA OF OKHOTSK
Kamchatka
Sakhalin
KURIL ISLANDS
SEA OF JAPAN
JAPAN
Arctic Circle
Omsk
Novosibirsk
Krasnoyarsk
Irkutsk
Ulan-Ude
Chita
Yakutsk
Khabarovsk
Vladivostok
Dudinka
Archangel
Sverdlovsk
Chelyabinsk
Tashkent

ADMINISTRATIVE DIVISIONS

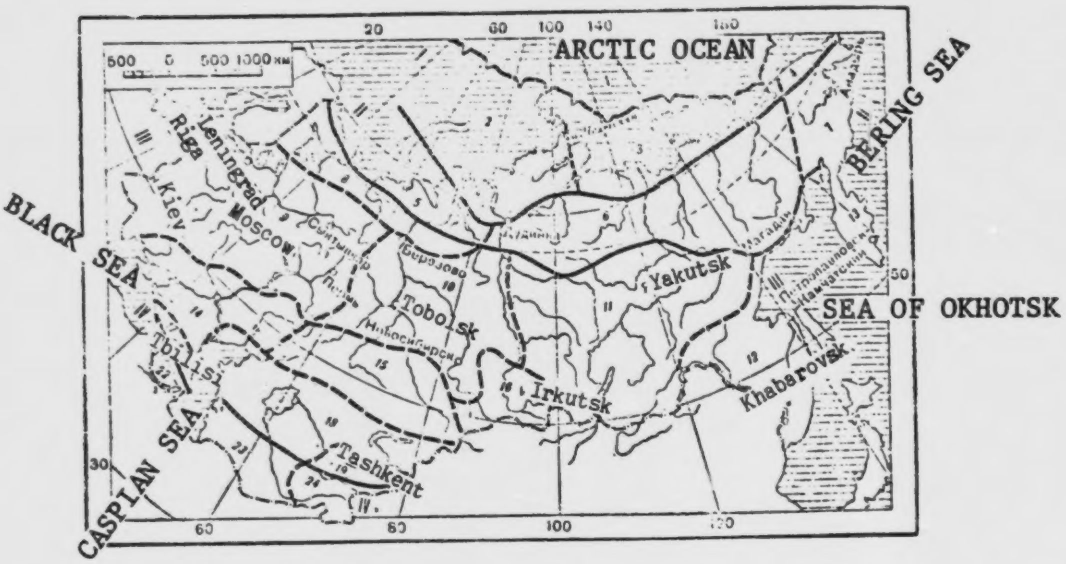
S.S.R.

1. R.S.F.S.R
2. Karelo-Finnish S.S.R.
3. Estonian S.S.R.
4. Latvian S.S.R.
5. Lithuanian S.S.R.
6. White Russian S.S.R.
7. Ukrainian S.S.R.
8. Moldavian S.S.R.
9. Georgian S.S.R.
10. Armenian S.S.R.
11. Azerbaydzhan S.S.R.
12. Kazakh S.S.R.
13. Uzbek S.S.R.
14. Turkmen S.S.R.
15. Tadzhik S.S.R.
16. Kirgiz S.S.R.

A.S.S.R.

A. Komi ASSR
B. Udmurtskaya ASSR
C. Mariyskaya ASSR
D. Chuvashskaya ASSR
E. Mordovskaya ASSR
F. Tatarskaya ASSR
G. Bashkirskaya ASSR
H. Dagestanskaya ASSR
J. Severo-Osetinskaya ASSR
K. Kabardinskaya ASSR
L. Abkhazskaya ASSR
M. Adzharskaya ASSR
N. Nakhichevanskaya ASSR
O. Kara-Kalpakskaya ASSR
P. Buryat-Mongol'skaya ASSR
Q. Yakutskaya ASSR

CLIMATIC ZONES AND REGIONS* OF THE USSR

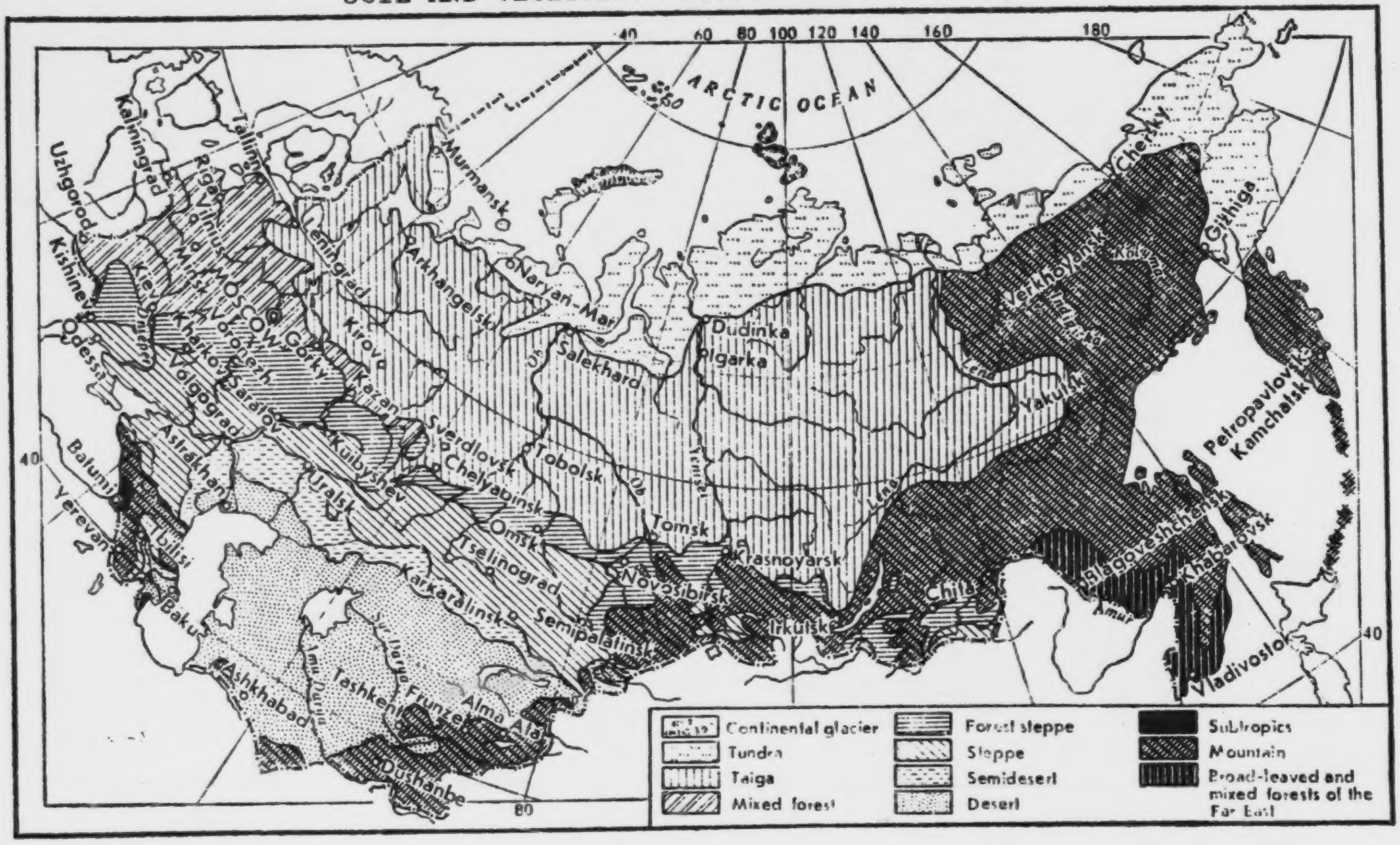


ARCTIC OCEAN
BERING SEA
BLACK SEA
SEA OF OKHOTSK
CASPIAN SEA
500 0 500 1000 км
Riga
Leningrad
Kiev
Moscow
Tobolsk
Yakutsk
Irkutsk
Khabarovsk
Tbilisi
Tashkent
I
II
III
IV
20
60
100
140
180
30
50
60
80
100
120

Zones: I-arctic, II-subarctic, III-temperate, IV-subtropical
Regions: 1-polar, 2-Atlantic, 3-East Siberian, 4-Pacific, 5-Atlantic, 6-Siberian, 7-Pacific, 8-Atlantic-arctic, 9-Atlantic-continental forests, 10-continental forests West Siberian, 11-continental forests East Siberian, 12-monsoon forests, 13-Pacific forests, 14-Atlantic-continental steppe, 15-continental steppe West Siberian, 16-mountainous Altay and Sayan, 17-mountainous Northern Caucasus, 18-continental desert Central Asian, 19-mountainous Tyan-Shan, 20-western Transcaucasian, 21-eastern Transcaucasian, 22-mountainous Transcaucasian highlands, 23-desert south-Turanian, 24-mountainous Pamir-Alay

(After B. P. Alisov, "Climate of The USSR", Moscow 1956)

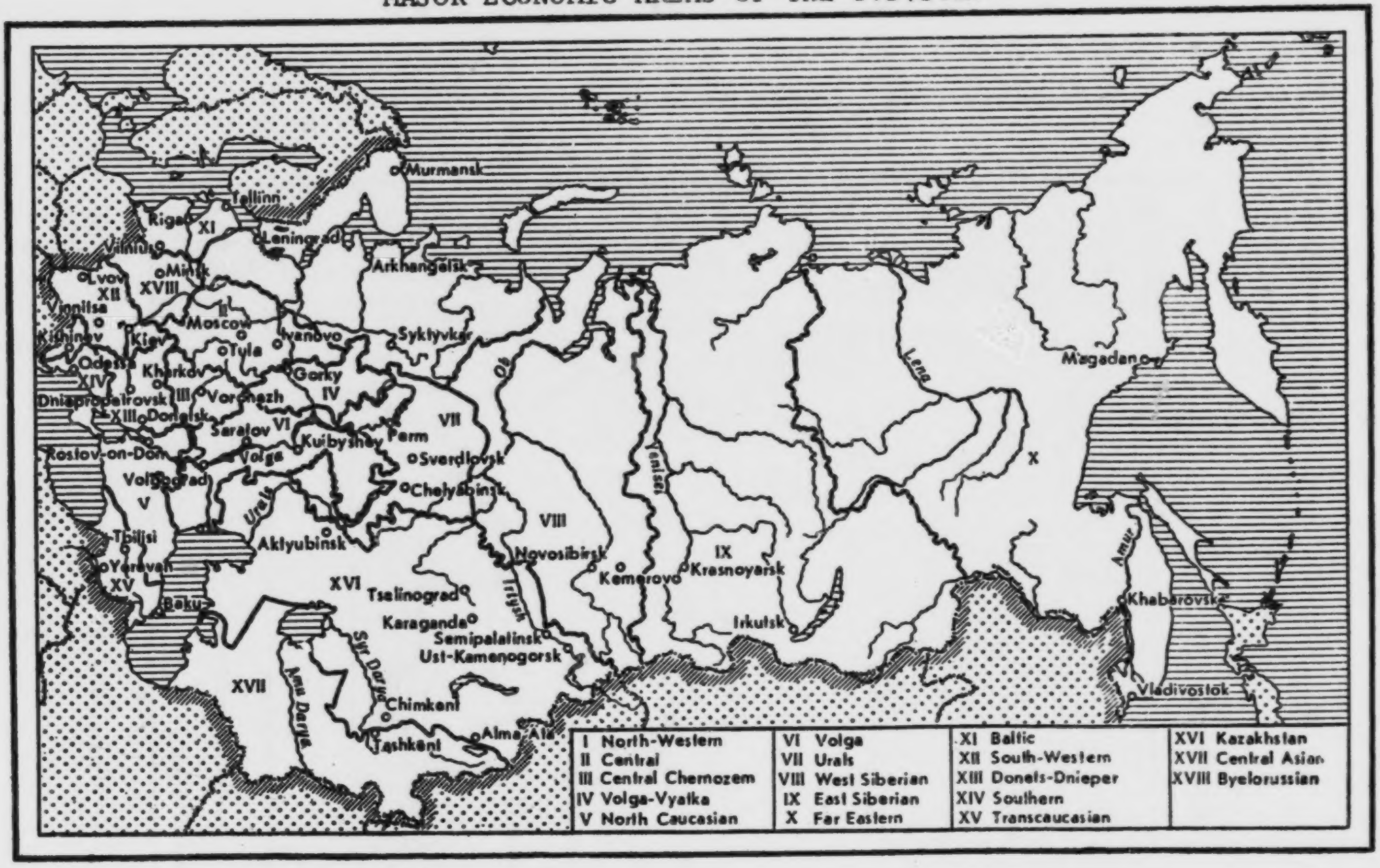
SOIL AND VEGETATION ZONES IN THE U.S.S.R.



ARCTIC OCEAN
Continental glacier
Tundra
Taiga
Mixed forest
Forest steppe
Steppe
Semidesert
Desert
Subtropics
Mountain
Broad-leaved and mixed forests of the Far East
Murmansk
Leningrad
Arkhangelsk
Naryan-Mar
Dudinka
Igarka
Salekhard
Kirov
Kazan
Gorky
Moscow
Kiev
Kharkov
Voronezh
Saratov
Volgograd
Odessa
Kishinev
Uzhgorod
Kaliningrad
Riga
Tallinn
Vilnius
Minsk
Astrakhan
Batumi
Yerevan
Tbilisi
Baku
Ashkhabad
Tashkent
Frunze
Alma Ata
Dushanbe
Uralsk
Kuibyshev
Sverdlovsk
Chelyabinsk
Tobolsk
Omsk
Tselinograd
Karkaralinsk
Semipalatinsk
Novosibirsk
Tomsk
Krasnoyarsk
Irkutsk
Chita
Yakutsk
Verkhoyansk
Blagoveshchensk
Khabarovsk
Vladivostok
Petropavlovsk Kamchatsky
Gizhiga
Chersky
Amur
40
60
80
100
120
140
160
180

(After A. Lavrishchev, "Economic Geography of the U.S.S.R.", Moscow 1969)

MAJOR ECONOMIC AREAS OF THE U.S.S.R.


Murmansk
Tallinn
Riga
XI
Leningrad
Vilnius
Minsk
Lvov
XII
XVIII
Arkhangelsk
Vinnitsa
II
Moscow
Ivanovo
Syktyvkar
Kishinev
Kiev
Tula
Odessa
XIV
Kharkov
III
Voronezh
Gorky
IV
Dnepropetrovsk
XIII
Donetsk
Saratov
VI
Kuibyshev
Perm
VII
Sverdlovsk
Rostov-on-Don
Volga
Volgograd
V
Chelyabinsk
Urals
Tbilisi
Aktyubinsk
Yerevan
XV
Baku
XVI
VIII
Novosibirsk
Ob
Yenisei
Lena
IX
Kemerovo
Krasnoyarsk
Tselinograd
Irtysh
Karaganda
Semipalatinsk
Ust-Kamenogorsk
Irkutsk
XVII
Syr Darya
Amu Darya
Chimkent
Alma-Ata
Tashkent
X
Magadan
Amur
Khabarovsk
Vladivostok
I North-Western
II Central
III Central Chernozem
IV Volga-Vyatka
V North Caucasian
VI Volga
VII Urals
VIII West Siberian
IX East Siberian
X Far Eastern
XI Baltic
XII South-Western
XIII Donets-Dnieper
XIV Southern
XV Transcaucasian
XVI Kazakhstan
XVII Central Asian
XVIII Byelorussian

PLANNED DISTRIBUTION OF INDUSTRIAL PRODUCTION IN ORDER TO BRING IT CLOSER TO RAW MATERIAL AND FUEL SOURCES

An example of the planned distribution of industrial production in the USSR is the creation of large industrial centers and complexes of heavy industry in many of the country's economic areas: the North-West (Kirovsk, Kandalaksha, Vorkuta), the Urals (Magnitogorsk, Chelyabinsk, Nizhny Tagil), Western and Eastern Siberia (Novosibirsk, Novokuznetsk, Kemerovo, Krasnoyarsk, Irkutsk, Bratsk), Kazakhstan (Karaganda, Rudny, Balkhash, Dzhezkazgan).

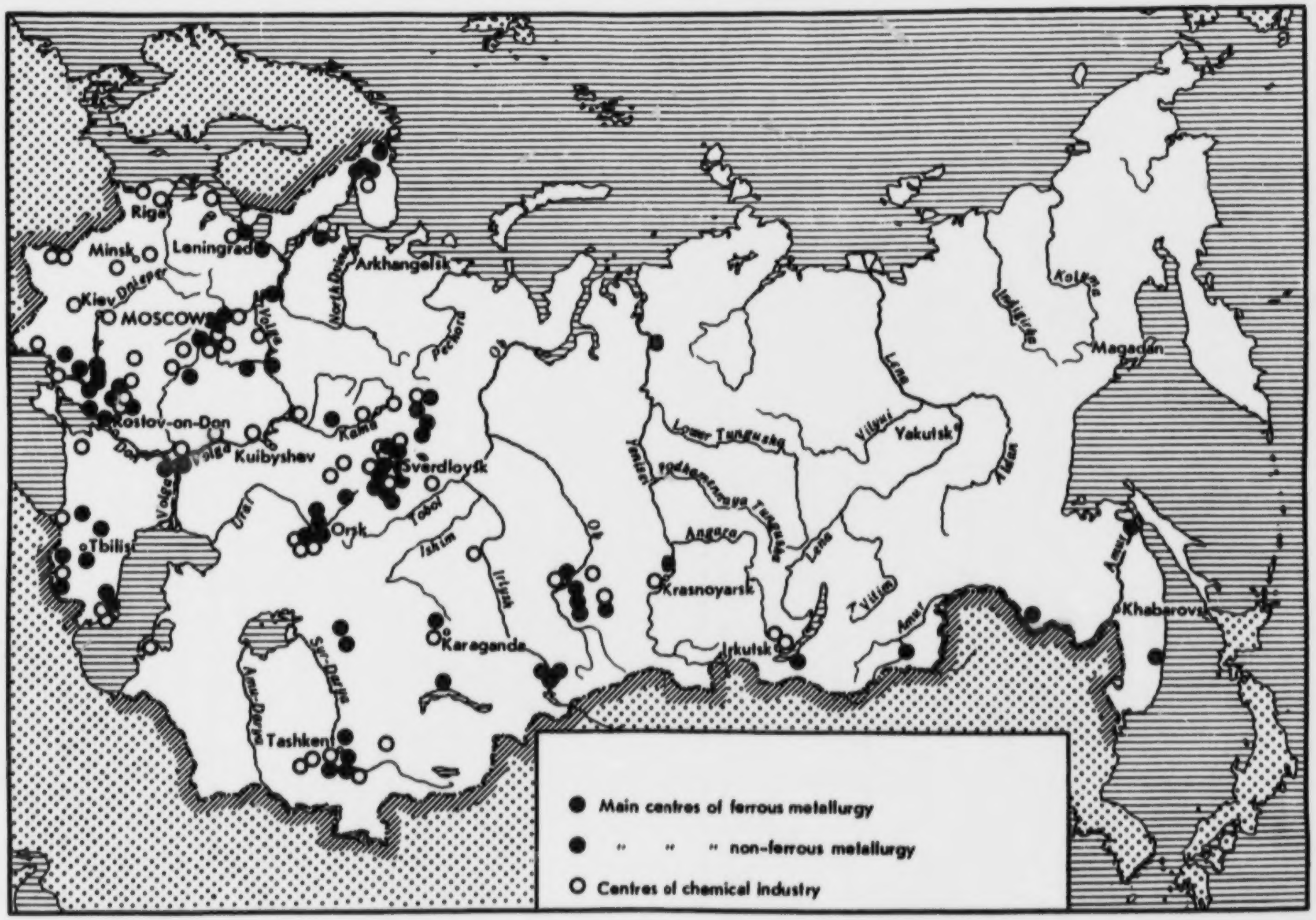
Large industrial systems are being created - Kustanai, Pavlodar-Ekibastuz, Achinsk-Krasnoyarsk, Bratsk-Taishet and a number of others. Ferrous and non-ferrous metallurgy, pulp and paper, hydrolysis and saw-milling industries are being established in the Bratsk-Taishet industrial system. The Achinsk-Krasnoyarsk industrial system is becoming one of the largest centers of aluminum and chemical industries, and production of ferrous metals, cellulose, paper, and oil products.

Construction of the third metallurgical base has been launched in Siberia, and a new base of ferrous metallurgy, using the enormous local iron and coal resources, has been created in Kazakhstan. A high-capacity power system is being organized in the same areas. Non-ferrous metallurgy is being further developed in Kazakhstan, Central Asia and in Transbaikal areas. The pulp and paper, as well as the timber, industries are being developed at a fast rate in the forest areas of Siberia and the Far East.

Ferrous metallurgy is also developing in the European part of the country by utilizing the enormous iron ore resources of the Kursk Magnetic Anomaly and the Ukrainian deposits. Large new production systems are under construction in the North-West, along the Volga, in the Northern Caucasus and the Ukraine.

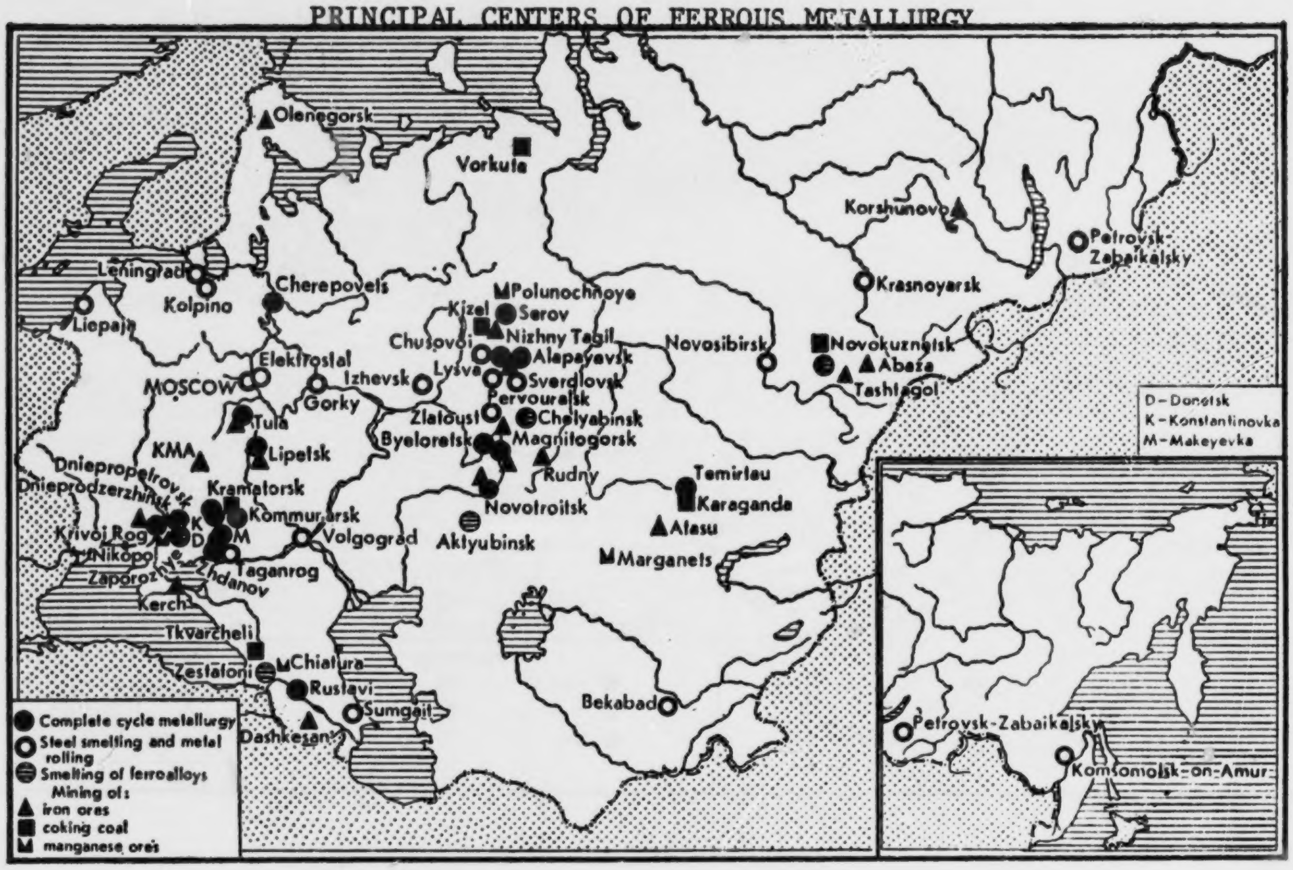
(After A. Lavrishchev, "Economic Geography
of the U.S.S.R.", Moscow 1969)

THE MAJOR INDUSTRIAL CENTERS OF THE USSR

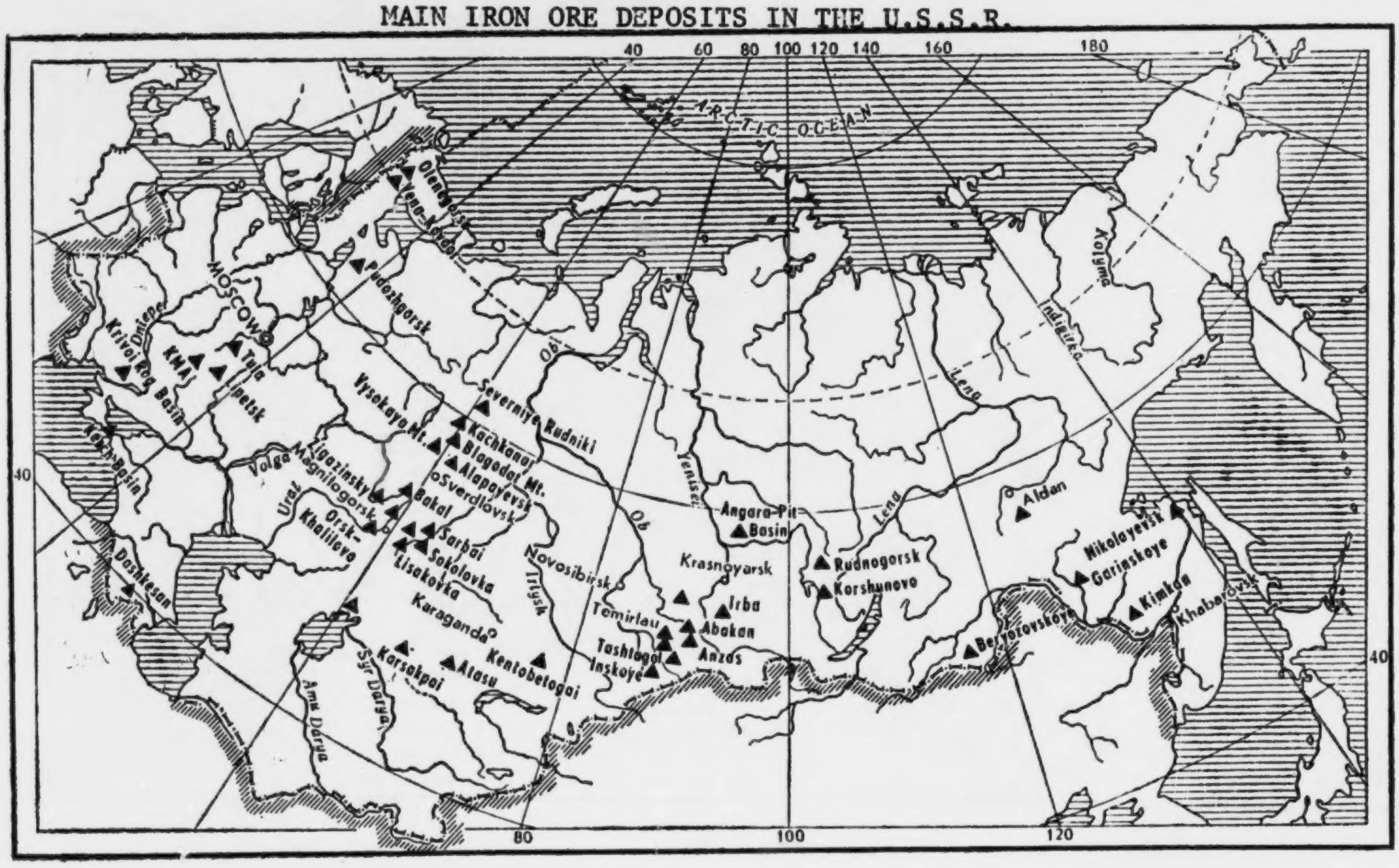

Riga
Minsk
Leningrad
Kiev
Dnieper
MOSCOW
Volga
North Dvina
Arkhangelsk
Pechora
Ob
Rostov-on-Don
Don
Volga
Kuibyshev
Kama
Sverdlovsk
Volga
Ural
Orsk
Tobol
Ishim
Irtysh
Tbilisi
Karaganda
Syr-Darya
Amu-Darya
Tashkent
Ob
Yenisei
Lower Tunguska
Podkamennaya Tunguska
Angara
Krasnoyarsk
Irkutsk
Lena
Vilyui
Yakutsk
Aldan
Vitim
Amur
Amur
Khabarovsk
Indigirka
Kolyma
Magadan
● Main centres of ferrous metallurgy
● " " " non-ferrous metallurgy
○ Centres of chemical industry

(After A. Efimov, "Soviet Industry", Moscow 1968)

PRINCIPAL CENTERS OF FERROUS METALLURGY


Olenegorsk
Vorkuta
Korshunovo
Petrovsk-Zabaikalsky
Leningrad
Kolpino
Cherepovets
Liepaja
Polunochnoye
Kizel
Serov
Nizhny Tagil
Chusovoi
Alapayevsk
Lysva
Sverdlovsk
Izhevsk
Pervouralsk
Zlatoust
Chelyabinsk
Byeloretsk
Magnitogorsk
Rudny
Novotroitsk
Aktyubinsk
Krasnoyarsk
Novosibirsk
Novokuznetsk
Abaza
Tashtagol
Elektrostal
MOSCOW
Gorky
Tula
KMA
Lipetsk
Dniepropetrovsk
Dnieprodzerzhinsk
Kramatorsk
Kommunarsk
Krivoi Rog
Nikopol
Zaporozhye
Zhdanov
Taganrog
Volgograd
Kerch
Tkvarcheli
Zestafoni
Chiatura
Rustavi
Sumgait
Dashkesan
Temirtau
Karaganda
Atasu
Marganets
Bekabad
K
D
M
D – Donetsk
K – Konstantinovka
M – Makeyevka
Petrovsk-Zabaikalsky
Komsomolsk-on-Amur
● Complete cycle metallurgy
○ Steel smelting and metal rolling
⊖ Smelting of ferroalloys
Mining of:
▲ iron ores
■ coking coal
M manganese ores

MAIN IRON ORE DEPOSITS IN THE U.S.S.R.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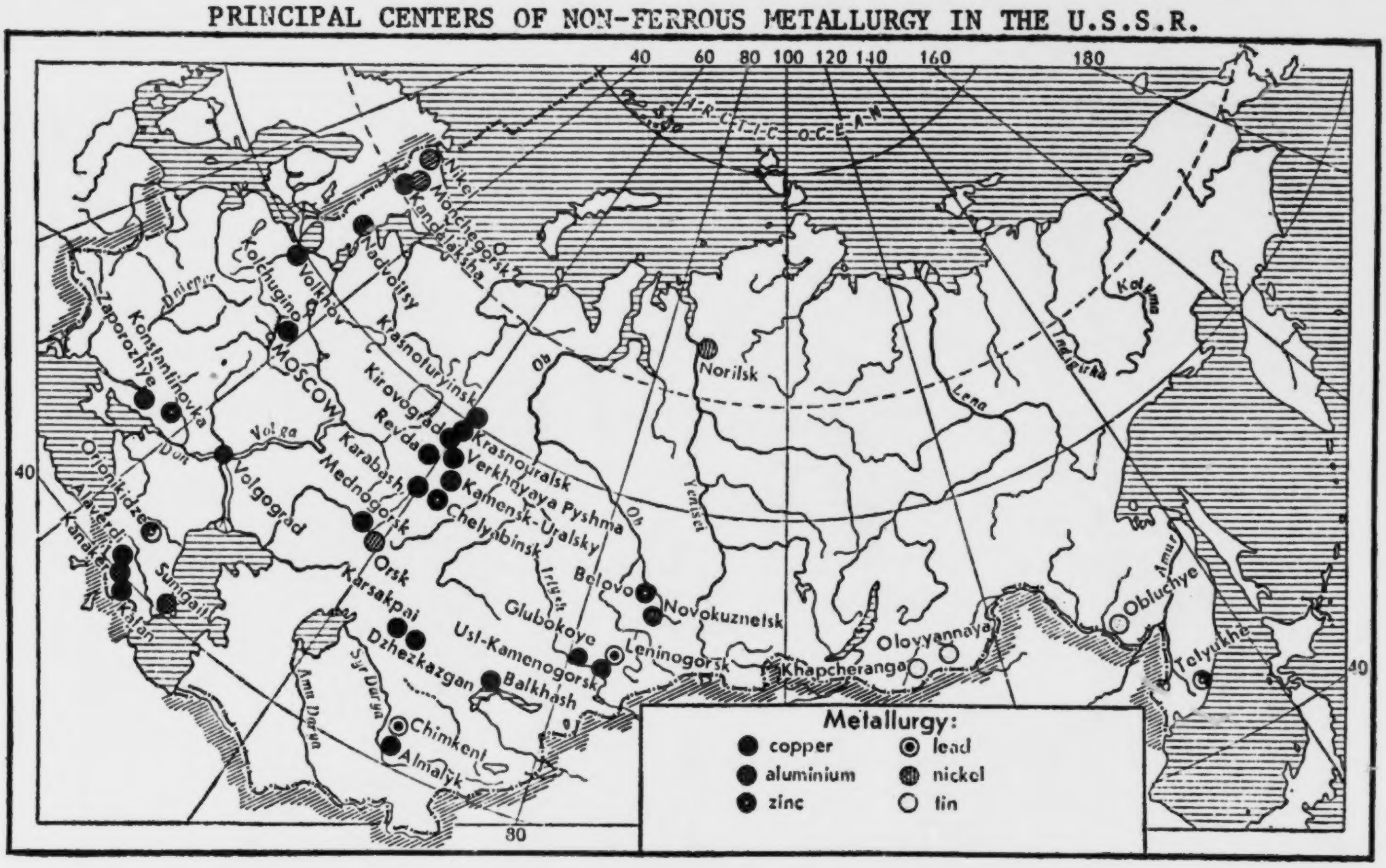
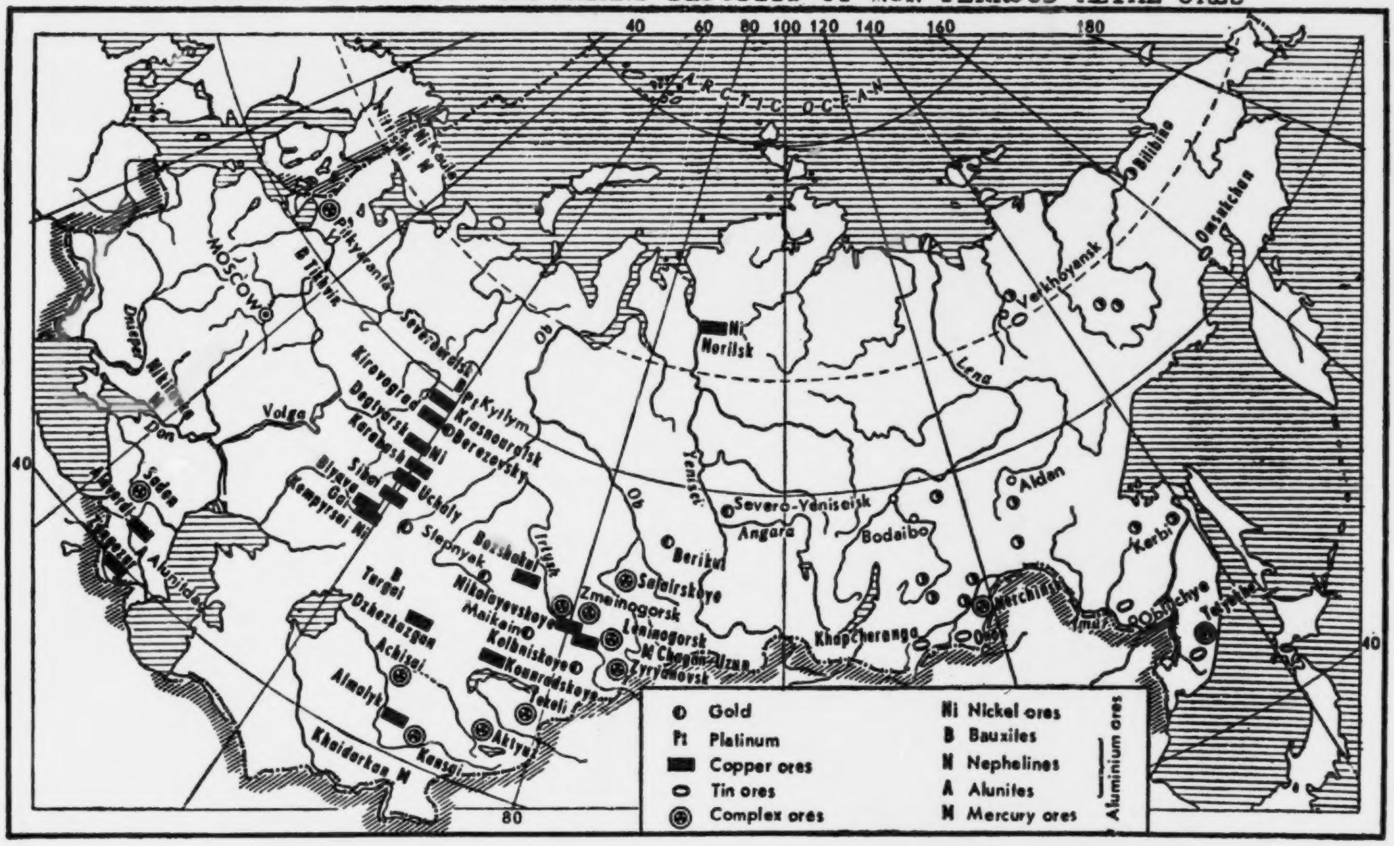
140
160
180
ARCTIC OCEAN
Olenegorsk
Yena-Kovdor
Pudozhgorsk
MOSCOW
Dnieper
Krivoi Rog Basin
KMA
Tula
Lipetsk
Kerch Basin
Vysokaya Mt.
Severnye Rudniki
Kachkanar
Blagodat Mt.
Alapayevsk
Sverdlovsk
Zlatoust
Magnitogorsk
Volga
Ural
Bakal
Orsk-Khalilovo
Sarbai
Sokolovka
Lisakovka
Dashkesan
Karaganda
Karsakpai
Atasu
Kentobetagai
Syr Darya
Amu Darya
Ob
Irtysh
Novosibirsk
Temirtau
Tashtagol
Inskoye
Abakan
Anzas
Irba
Krasnoyarsk
Yenisei
Angara-Pit Basin
Rudnogorsk
Korshunovo
Lena
Aldan
Berezovskoye
Nikolayevsk
Garinskoye
Kimkan
Khabarovsk
Indigirka
Kolyma
40
80
100
120

(After A. Lavrishchev, "Economic Geography of the U.S.S.R.", Moscow 1969)

PRINCIPAL CENTERS OF NON-FERROUS METALLURGY IN THE U.S.S.R.

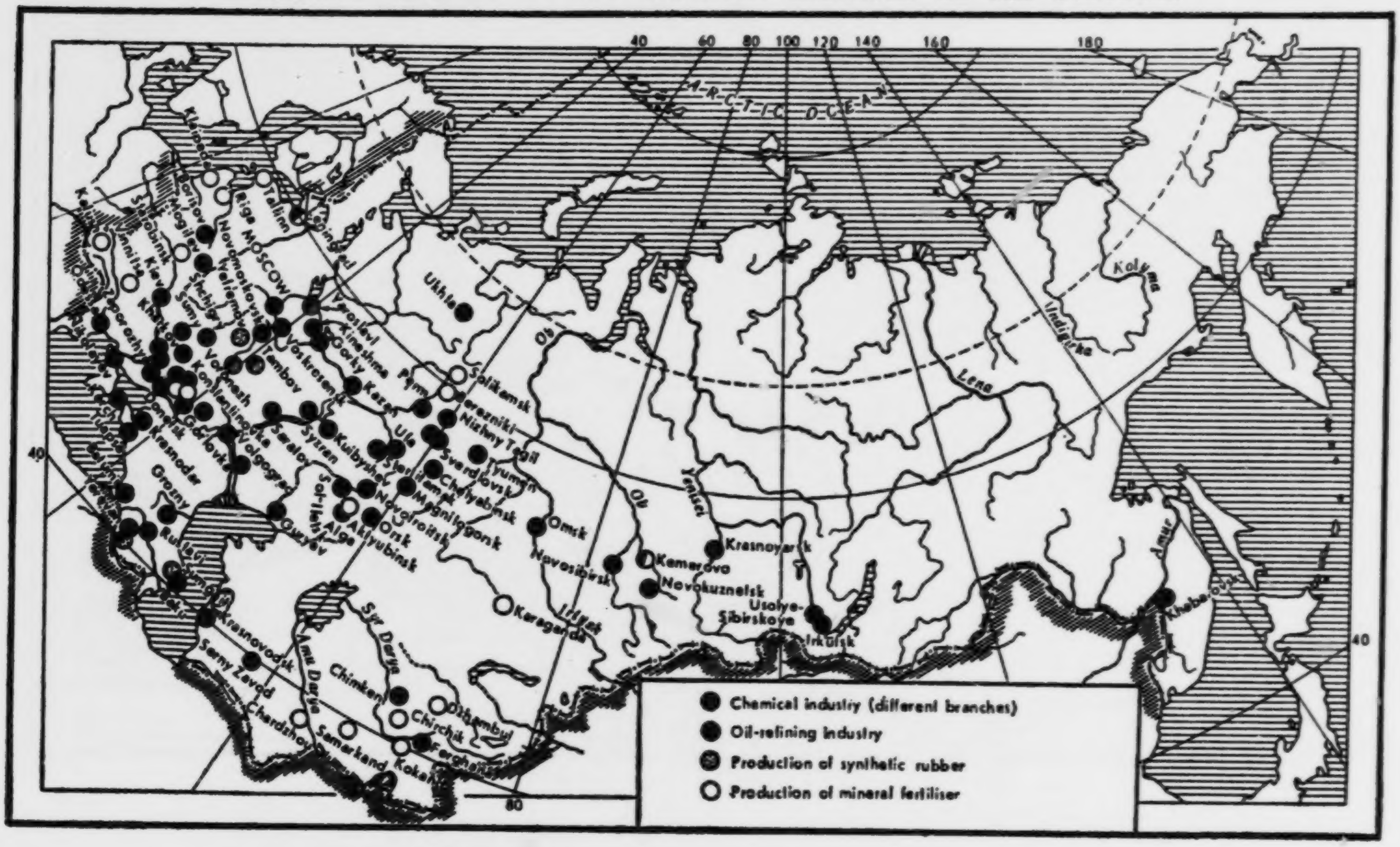

ARCTIC OCEAN
40
60
80
100
120
140
160
180
30
Nikel
Monchegorsk
Kandalaksha
Nadvoitsy
Volkhov
Kolchugino
MOSCOW
Dnieper
Zaporozhye
Konstantinovka
Volga
Don
Volgograd
Ordzhonikidze
Alaverdi
Kanaker
Sumgait
Kirovograd
Krasnoturyinsk
Krasnouralsk
Revda
Verkhnyaya Pyshma
Karabash
Kamensk-Uralsky
Mednogorsk
Chelyabinsk
Orsk
Karsakpai
Dzhezkazgan
Balkhash
Chimkent
Almalyk
Syr Darya
Amu Darya
Irtysh
Ob
Yenisei
Norilsk
Lena
Kolyma
Indigirka
Belovo
Novokuznetsk
Glubokoye
Ust-Kamenogorsk
Leninogorsk
Khapcheranga
Olovyannaya
Obluchye
Amur
Tetyukhe
Metallurgy:
● copper
● aluminium
● zinc
◉ lead
● nickel
○ tin

DISTRIBUTION OF MOST IMPORTANT DEPOSITS OF NON-FERROUS METAL ORES

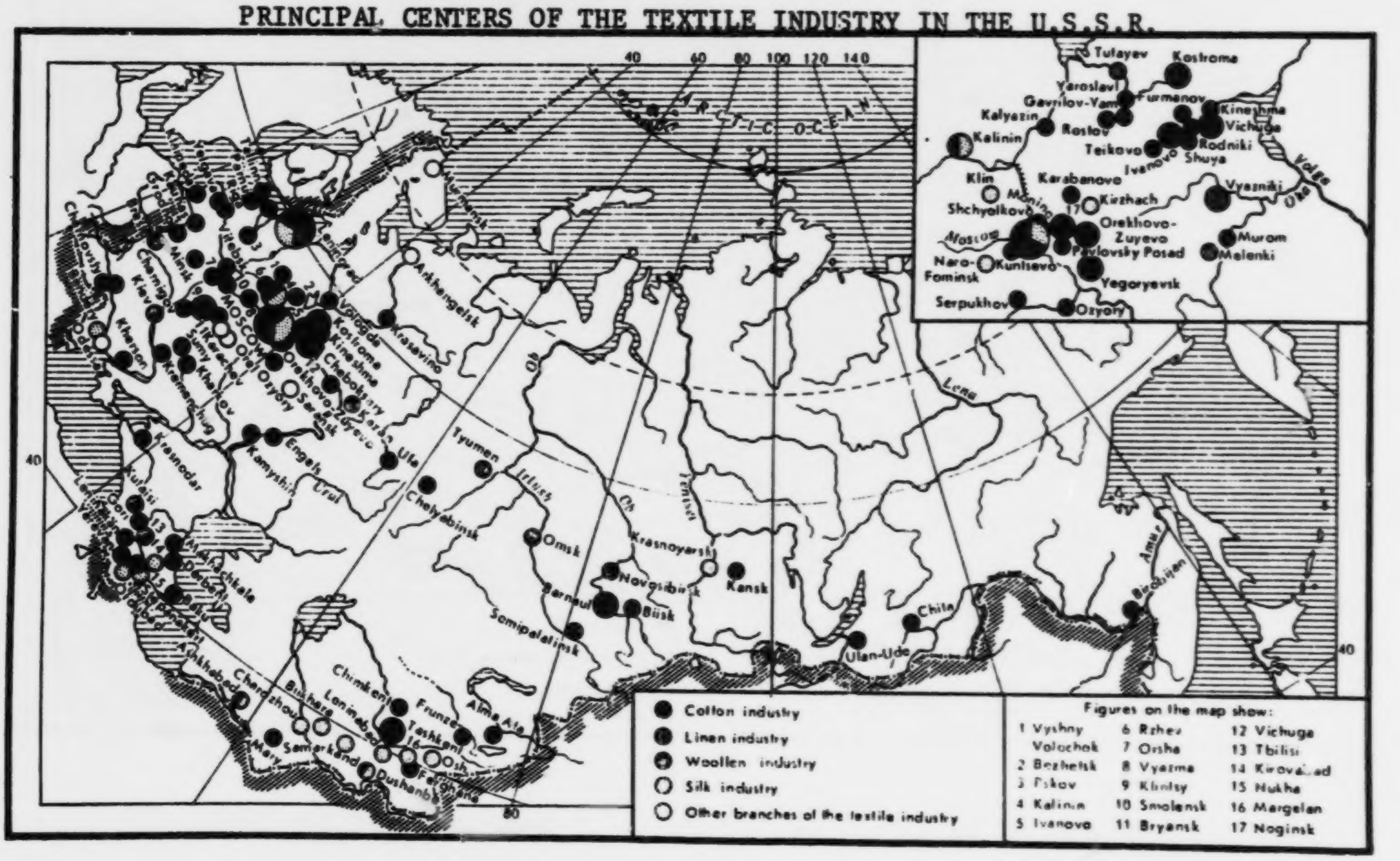

ARCTIC OCEAN
40
60
80
100
120
140
160
180
80
MOSCOW
Dnieper
Volga
Don
Nikopol
B Tikhvin
Kirovograd
Krasnouralsk
Berezovsky
Degtyarsk
Karabash
Sibai
Uchaly
Stepnyak
Sadon
Alaverdi
Alunite
Turgai
Dzhezkazgan
Achisai
Almalyk
Kensai
Khaidarkan
Nikolayevskoye
Maikain
Kolbinskoye
Kounradskoye
Tekeli
Aktyuz
Zmeinogorsk
Leninogorsk
Chagan-Uzun
Zyryanovsk
Salairskoye
Berikul
Ob
Irtysh
Yenisei
Angara
Severo-Yeniseisk
Norilsk
Ni
Bodaibo
Lena
Aldan
Verkhoyansk
Bilibino
Omsukchan
Khapcheranga
Nerchinsk
Amur
Kerbi
Obluchye
Tetyukhe
Gold
Pt Platinum
Copper ores
Tin ores
Complex ores
Ni Nickel ores
B Bauxites
N Nephelines
A Alunites
M Mercury ores
Aluminium ores

(After A. Lavrishchev, "Economic Geography of the U.S.S.R.", Moscow 1969)

PRINCIPAL CENTERS OF THE CHEMICAL INDUSTRY IN THE U.S.S.R.

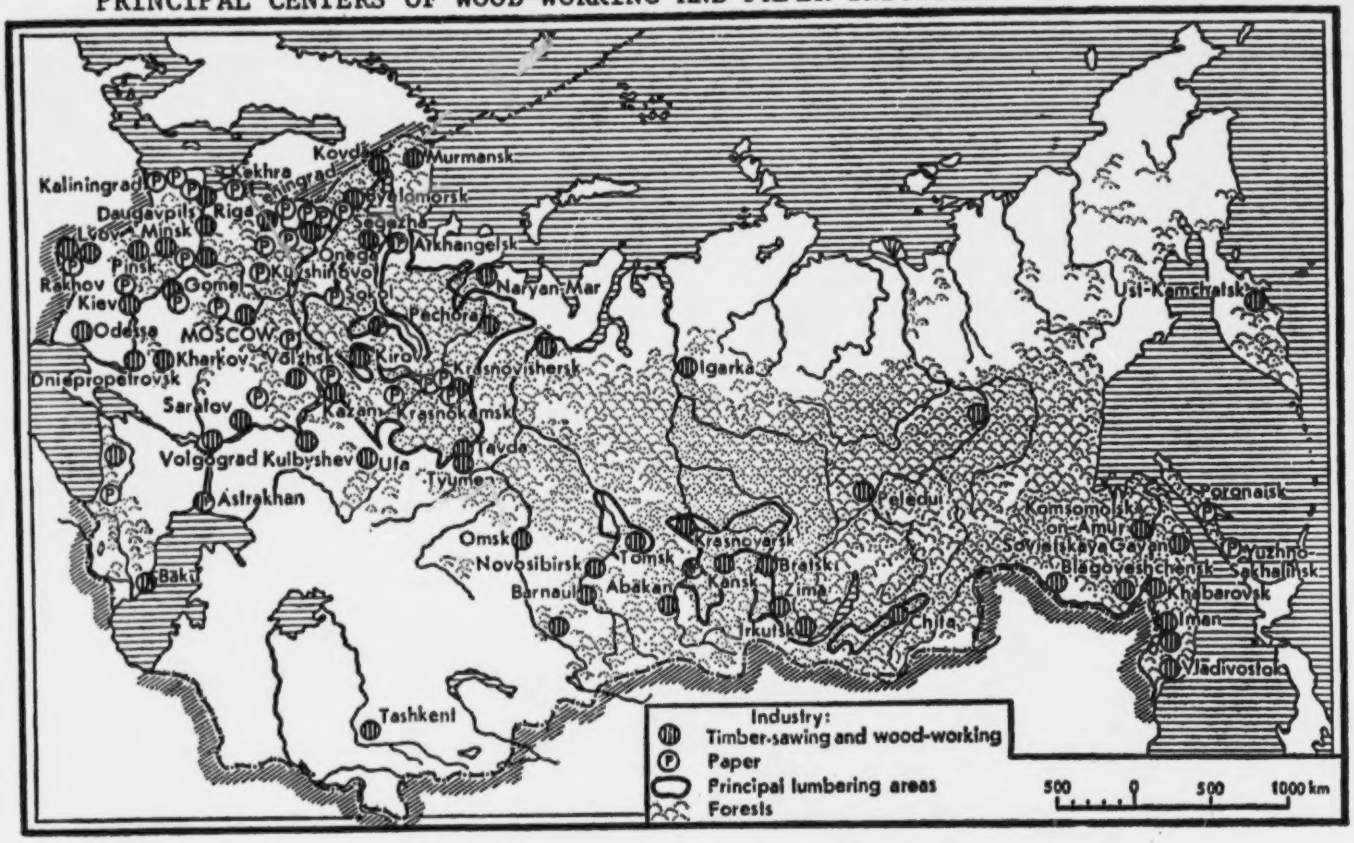

ARCTIC OCEAN
Chemical industry (different branches)
Oil-refining industry
Production of synthetic rubber
Production of mineral fertiliser
Omsk
Novosibirsk
Kemerovo
Novokuznetsk
Krasnoyarsk
Usolye-Sibirskoye
Irkutsk
Karaganda
Chimkent
Chirchik
Dzhambul
Samarkand
Krasnovodsk
Sverdlovsk
Chelyabinsk
Magnitogorsk
Orsk
Aktyubinsk
Solikamsk
Berezniki
Nizhny Tagil
Ufa
Kuibyshev
Kazan
Gorky
Yaroslavl
MOSCOW
Voskresensk
Grozny
Krasnodar
Kolyma
Indigirka
Lena
Yenisei
Ob
Amur
Khabarovsk
Irtysh
Syr Darya
Amu Darya

PRINCIPAL CENTERS OF THE TEXTILE INDUSTRY IN THE U.S.S.R.

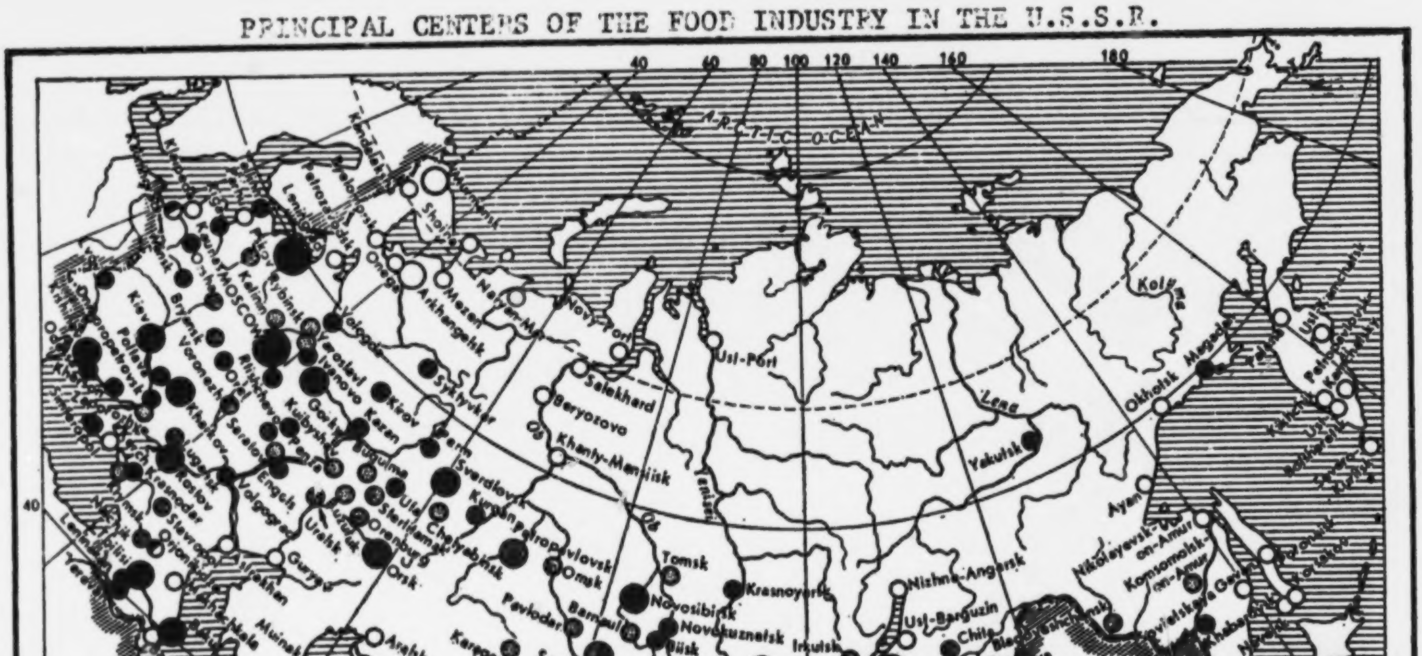

ARCTIC OCEAN
Tutayev
Kostroma
Yaroslavl
Gavrilov-Yam
Furmanov
Kalyazin
Rostov
Kineshma
Vichuga
Kalinin
Teikovo
Rodniki
Ivanovo
Shuya
Klin
Karabanovo
Kirzhach
Vyazniki
Shchyolkovo
Orekhovo-Zuyevo
Pavlovsky Posad
Moscow
Murom
Melenki
Naro-Fominsk
Kuntsevo
Yegoryevsk
Serpukhov
Ozyory
Volga
Oka
Arkhangelsk
Krasavino
Tyumen
Chelyabinsk
Omsk
Krasnoyarsk
Kansk
Novosibirsk
Barnaul
Biisk
Semipalatinsk
Ulan-Ude
Chita
Birobijan
Frunze
Alma Ata
Tashkent
Chimkent
Samarkand
Dushanbe
Engels
Kamyshin
Krasnodar
Cotton industry
Linen industry
Woollen industry
Silk industry
Other branches of the textile industry
Figures on the map show:
1 Vyshny Volochok
2 Bezhetsk
3 Pskov
4 Kalinin
5 Ivanovo
6 Rzhev
7 Orsha
8 Vyazma
9 Klintsy
10 Smolensk
11 Bryansk
12 Vichuga
13 Tbilisi
14 Kirovabad
15 Nukha
16 Margelan
17 Noginsk

(After A. Lavrishchev, "Economic Geography of the U.S.S.R.", Moscow 1969)

PRINCIPAL CENTERS OF WOOD-WORKING AND PAPER INDUSTRIES IN THE U.S.S.R.

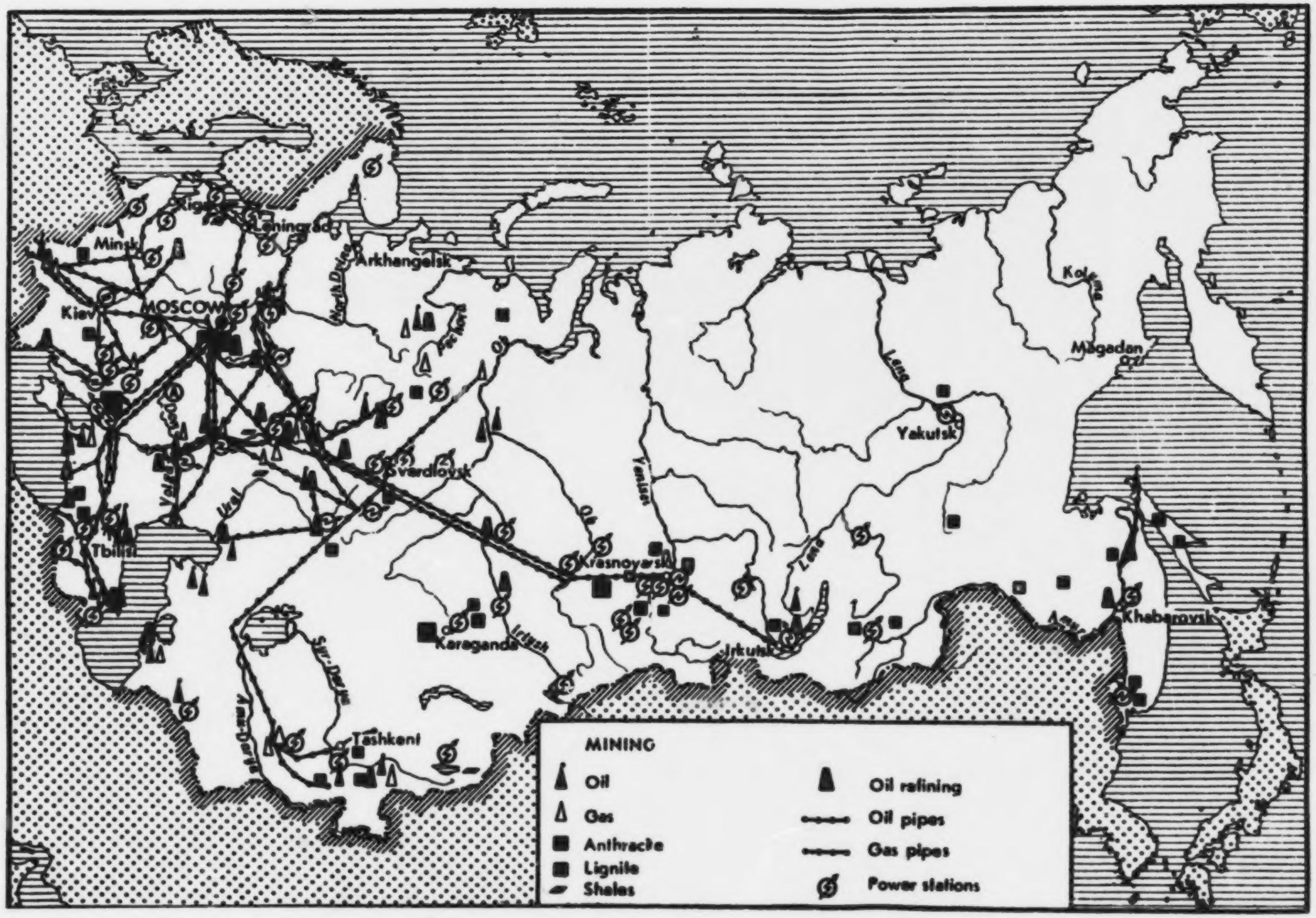

Industry:
Ⓘ Timber-sawing and wood-working
Ⓟ Paper
Principal lumbering areas
Forests
500 0 500 1000 km
Murmansk
Kovda
Kaliningrad
Kekhra
Daugavpils
Riga
Lvov
Minsk
Belomorsk
Segezha
Onega
Arkhangelsk
Pinsk
Rakhov
Kiev
Gomel
Kuvshinovo
Naryan-Mar
Pechora
Odessa
MOSCOW
Kharkov
Volzhsk
Kirov
Krasnovishersk
Dniepropetrovsk
Saratov
Kazan
Krasnokamsk
Volgograd
Kuibyshev
Ufa
Tavda
Tyumen
Astrakhan
Baku
Omsk
Novosibirsk
Barnaul
Tomsk
Abakan
Igarka
Krasnoyarsk
Kansk
Bratsk
Zima
Irkutsk
Chita
Peledui
Tashkent
Ust-Kamchatsk
Poronaisk
Komsomolsk-on-Amur
Sovietskaya Gavan
Blagoveshchensk
Yuzhno-Sakhalinsk
Khabarovsk
Iman
Vladivostok

PRINCIPAL CENTERS OF THE FOOD INDUSTRY IN THE U.S.S.R.


● Food industry
● Flour-milling industry
● Meat industry
○ Fish and fish packing industry
ARCTIC OCEAN
40
60
80
100
120
140
160
180
Murmansk
Arkhangelsk
Naryan-Mar
Salekhard
Beryozovo
Khanty-Mansiisk
Ust-Port
Kolyma
Magadan
Okhotsk
Yakutsk
Lena
Ayan
MOSCOW
Kiev
Voronezh
Volgograd
Astrakhan
Krasnodar
Saratov
Kuibyshev
Kazan
Kirov
Perm
Sverdlovsk
Ufa
Chelyabinsk
Orenburg
Orsk
Guryev
Petropavlovsk
Omsk
Tomsk
Novosibirsk
Krasnoyarsk
Barnaul
Novokuznetsk
Biisk
Pavlodar
Semipalatinsk
Karaganda
Aralsk
Muinak
Tashkent
Chimkent
Alma-Ata
Frunze
Osh
Leninabad
Samarkand
Ashkhabad
Dushanbe
Irkutsk
Kyzyl
Ulan-Ude
Ust-Barguzin
Nizhne-Angarsk
Chita
Nikolayevsk-on-Amur
Komsomolsk-on-Amur
Sovietskaya Gavan
Khabarovsk
Vladivostok
Nakhodka
Ussuriisk
Yuzhno-Sakhalinsk
Poronaisk
Petropavlovsk-Kamchatsky
Ust-Kamchatsk

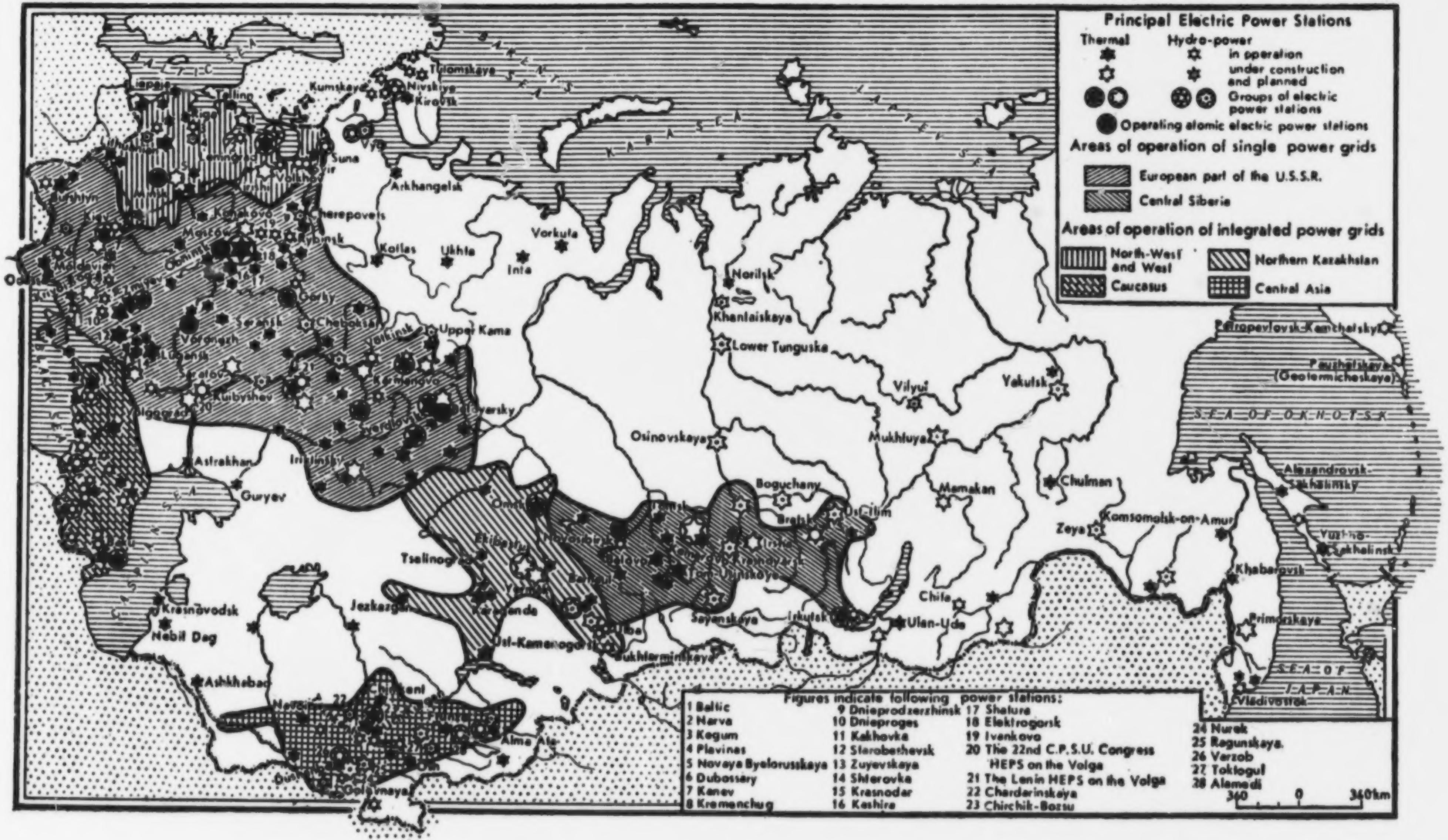
(After A. Lavrishchev, "Economic Geography
of the U.S.S.R.", Moscow 1969)

THE MAIN MINING CENTERS OF THE USSR


Riga
Leningrad
Minsk
Arkhangelsk
North Dvina
Kiev
MOSCOW
Volga
Don
Ural
Sverdlovsk
Tbilisi
Ob
Yenisei
Krasnoyarsk
Irtysh
Karaganda
Syr-Darya
Amu-Darya
Tashkent
Irkutsk
Lena
Yakutsk
Kolyma
Magadan
Amur
Khabarovsk
MINING
Oil
Gas
Anthracite
Lignite
Shales
Oil refining
Oil pipes
Gas pipes
Power stations

(After A. Efimov, "Soviet Industry", Moscow 1968)

PRINCIPAL ELECTRIC POWER STATIONS AND POWER SYSTEMS IN THE U.S.S.R.


Principal Electric Power Stations
Thermal
Hydro-power
in operation
under construction and planned
Groups of electric power stations
Operating atomic electric power stations
Areas of operation of single power grids
European part of the U.S.S.R.
Central Siberia
Areas of operation of integrated power grids
North-West and West
Northern Kazakhstan
Caucasus
Central Asia
Figures indicate following power stations:
1 Baltic
2 Narva
3 Kegum
4 Plavinas
5 Novaya Byelorusskaya
6 Dubossary
7 Kanev
8 Kremenchug
9 Dnieprodzerzhinsk
10 Dnieproges
11 Kakhovka
12 Starobeshevsk
13 Zuyevskaya
14 Shterovka
15 Krasnodar
16 Kashira
17 Shatura
18 Elektrogorsk
19 Ivankovo
20 The 22nd C.P.S.U. Congress HEPS on the Volga
21 The Lenin HEPS on the Volga
22 Chardarinskaya
23 Chirchik-Bozsu
24 Nurek
25 Regunskaya
26 Varzob
27 Toktogul
28 Alamedi
360
0
360km
BALTIC SEA
BARENTS SEA
KARA SEA
LAPTEV SEA
SEA OF OKHOTSK
SEA OF JAPAN
CASPIAN SEA
BLACK SEA
Tulomskaya
Nivskiye
Kirovsk
Kumskaya
Liepaja
Tallinn
Suna
Arkhangelsk
Cherepovets
Kakhovo
Moscow
Rybinsk
Kotlas
Ukhta
Vorkuta
Inta
Gorky
Cheboksary
Votkinsk
Upper Kama
Voronezh
Lugansk
Saratov
Kuibyshev
Volgograd
Sverdlovsk
Beloyarsky
Astrakhan
Iriklinsky
Guryev
Krasnovodsk
Nebit Dag
Ashkhabad
Tselinograd
Jezkazgan
Ekibastuz
Karaganda
Ust-Kamenogorsk
Bukhtarminskaya
Alma-Ata
Golovnaya
Omsk
Novosibirsk
Barnaul
Norilsk
Khantaiskaya
Lower Tunguska
Osinovskaya
Boguchany
Bratsk
Ust-Ilim
Sayanskaya
Irkutsk
Ulan-Ude
Vilyui
Mukhtuya
Yakutsk
Mamakan
Chita
Chulman
Zeya
Komsomolsk-on-Amur
Khabarovsk
Primorskaya
Vladivostok
Alexandrovsk-Sakhalinsky
Yuzhno-Sakhalinsk
Petropavlovsk-Kamchatsky
Paushetskaya (Geotermicheskaya)

(After A. Lavrishchev, "Economic Geography of the U.S.S.R.", Moscow 1969)

PHYSIOLOGICAL-BIOCHEMICAL PRINCIPLES OF THE GAS RESISTANCE OF PLANTS

V. S. Nikolayevskiy

From Ministerstvo Vysshego i Srednego Spetsial'nogo Obrazovaniya RSFSR. Permskiy ordena trudovogo krasnogo znameni gosudarstvennyy universitet im. A. M. Gor'kogo. Uchenye Zapiski No. 222. "Gazoustoychivost' Rasteniy". Vypusk 1. Perm', p. 5-33, (1969).

Present State of The Problem of Gas Resistance of Plants

The problems of composition of atmospheric air and of effect of toxic gases on living organisms were debated even by ancient thinkers: Lucretius describes places near Avernus, Italy, which caused overflying birds to suffocate and fall. He gave a completely materialistic explanation for this phenomenon: poisonous gases escaping from the ground can either spoil the air or dilute it, causing birds to lose their lift. Areas around Avernus are rich in sulfur emissions (Mirtov, 1961).

Air pollution as a social problem arose at the beginning of the 14th century (Halliday, 1962), but the first studies were started at the beginning of the second half of the 19th century. An inevitable by-product of the development of industry and of civilization in the industrial areas of the countries of Europe, America and Asia was the appearance of polluted air and the formation of unproductive and poisoned land, where completely natural phytocoenoses (association of plants) were either seriously damaged or completely destroyed.

Enterprises of the ferrous and nonferrous metallurgy, as well as the chemical industry and the thermal electric power stations emit daily enormous amounts of various noxious gases (F_2, HF, Cl_2, SO_2, CO, N_2O_5, N_2O_3, H_2S, unsaturated hydrocarbons, metal oxides, etc.) and cause considerable damage to vegetation and to the animal world over vast surrounding areas. Major nonferrous metallurgical enterprises discharge up to 500 tons of sulfur dioxide per day, and each year, the emission of sulfur by industry and furnaces on the earth amounts to 60 million tons (Katz, quoted by Tomas, 1962).

The composition of noxious gases depends on the design of the enterprise and on the raw material it processes. The amount of gas discharged is determined by the output of the enterprise. The gas concentration in the ground layer of air depends on a whole set of weather-climatic and physical-geographical conditions prevailing in the region and also on the height of discharge of the gases, as well as on the hermetic tightness of the equipment and on the processes of dilution and sedimentation (Ryazanov, 1961 b). A combination of a lower gradient, calm, and an increased atmospheric humidity produces so-called temperature inversions (Ryazanov, 1961 b; Timofeyeva, Sadilova, and Kuperman, 1964), during which the gas clings to the ground, poisoning and destroying everything on its surface. The higher the temperature gradient, the lower the relative humidity of air, the higher the barometric pressure, and the more intense the solar radiation --- the stronger are the vertical air currents, and the greater the angle of opening of the smoke plume, and hence, the more vigorously proceeds the process of gas dilution.

The degree of the adverse effect of gases and the damage they cause to agriculture and forestry are very considerable. Thus, in the vicinity of major nonferrous enterprises and chemical plants, the radius of the air pollution zones is 17-25 km. In some cases, the effect of the gases is detected at a distance of 40 km or more from the smoke pollution source.

In view of the fact that atmospheric air is a major source of carbon nutrition of green plants, its pollution has a detrimental effect on their vital activity. Modern man has artificially created a new ecological factor that in its impact on plants is no less important than such factors as the drought or the salinization of soils. For example, the chief cause of the massive death of coniferous plantings in cities is the heavy pollution of air caused by the motor vehicle traffic.

Accumulations of gases and dust hang steadily in the atmosphere in the form of a cap over large cities and over industrial areas. During the morning and evening hours, the visibility is greatly reduced. At many industrial enterprises and in the cities of the Soviet Union (Timofeyeva, Sadilova, Kuperman, 1964; Nikolayevskiy, Kazantseva, 1966; Il'kun, 1968), Poland (Paluch, 1968), the U.S.A. (Tomas , 1962), and other countries, the air is polluted with a complex mixture of gases. In the U.S.A. and in England, the formation and action of smog (a mixture of gas, dust, and fog) has been described. A peculiar third type of smog occurring in the Ukraine was described by G. N. Il'kun (1968).

The disappearance of vegetation in the vicinity of industrial enterprises as well as cases of massive poisoning and death of people, birds, and animals (63 persons died in Maas, Belgium in 1930; in Donora, Pennsylvania [U.S.A.], in 1948, 6000 people were taken ill and 20 died; in London, England, in December 1952, a death rate increase of 4000 people as a result of smog was recorded) have attracted the attention not only of public health personnel but also of agricultural and forestry experts, botanists, and physiologists.

The first studies of the gas resistance of plants were initiated in Germany in 1861 (Wentzel, 1963), in Russia in 1900-1910 (Nelyubov, 1900, 1910; Sabashnikov, 1911), and in the U.S.A. in 1915-1920 (Fortunatov, 1958). Studies of the gas resistance of plants in the USSR were particularly expanded in the pre- and postwar years. Halliday (1962) estimates that during the postwar period, a total of about 150 papers devoted to the problem of gas resistance of plants are published every year throughout the world. In a number of countries of Central Europe there are periodic international conferences once every two years devoted to the problem of the "Influence of Polluted Air on Forests". The last conference was held on 9-14 September 1968 in the city of Katowice, Poland (Ed. note: The proceedings have been published largely in German and Polish). In the USSR an analogous conference was first held in Sverdlovsk in 1962 at the initiative of the Commission on the Conservation of Nature of the Ukrainian Branch of the Academy of Sciences, as well as of the Ural University and the Botanical Garden of the Biology Institute. This conference was held in connection with successful studies of the gas resistance of plants carried out at the copper smelting plants of the Central Ural by V. V. Tarchevskiy (1964 a, 1964). In 1964 and 1966, the second and third conferences were held in Sverdlovsk, and in 1968, the first Ukrainian conference took place in the city of Donetsk.

In view of the fact that the section of the botanical garden of the Institute of Biology of the Ukrainian Branch of the Academy of Sciences which dealt with the topic "Gas Resistance of Plants" was closed in 1966, we were compelled to transfer our studies to the botanical garden of Perm' State University (in the city of Perm') where the laboratory of "Experimental Ecology and Plant Acclimatization" was established. In the Ural, this is the only botanical garden conducting research on the problem of "Influence of polluted air on the life of plants growing in cities and industrial centers". Most of the papers in the present volume represent studies conducted by the laboratory staff in 1967 and 1968.

The investigation of the gas resistance of plants from the ecological standpoint is being conducted at the Bashkir State University by Yu. Z. Kulagin (1964 a, b, 1965, 1966 a, b, 1968). In addition, the gas resistance of plants is being studied in botanical gardens of Dnepropetrovsk State University (Babkina, 1968 a, b; Gayevaya, 1962), Kiev (Il'kun, Silayeva, Mironova, 1968), Donetsk (Panov, Rubtsov et al., 1968), Minsk (Getko, 1968), Karaganda (Sitnikova, 1964, 1966), at the Ukrainian Scientific Research Institute of the Academy of Municipal Services, Sverdlovsk (Kazantseva, 1965), at Donetsk State University (Negrutskaya, 1968; Negrutskiy, 1968), at the Krivoy Rog Pedagogical Institute (Dobrovol'skiy, 1968), and other institutions.

As was shown by the conferences held in Sverdkovsk (1962, 1964, 1966) and Donetsk (1968), these studies are being conducted by individual enthusiasts and groups of researchers and thus far there are no major institutions (with the exception of the Scientific Research Institute of Zabrze, Poland) which have done any extensive or thorough scientific research on the various aspects of the complex problem of conservation of nature, and on gas resistance of plants in particular. The necessity of establishing an institute of conservation of nature in the Ural Region is evident to all, since it is here that the effect of man on nature is manifested in its most varied forms.

Characteristics of Toxic Compounds and Permissible Air Pollution Norms

Industrial enterprises pollute the air with a great variety of toxic compounds. The diversity of the raw materials being processed and of the products obtained is matched by that of the ingredients polluting the biosphere. To date, there has been no scientifically developed classification for the toxic compounds polluting the air. Such a classification may be arrived at on the basis of two principles: 1 - physical and chemical composition of the compounds, and 2 - nature of their toxic action on plants.

From a physical standpoint, they can be divided into gases (simple and mixed) and vapors and dust (aerosols). Although, thus far, the chemical mechanism of their toxic action on plants has been little studied, these compounds can be arbitrarily divided into the following categories, taking into account their chemical properties: 1) acid gases (fluorine, chlorine, sulfur dioxide, carbon monoxide, carbon dioxide, nitrogen and phosphorus oxides, hydrogen sulfide); 2) vapors of acids (hydrochloric, hydrofluoric, sulfuric and sulfurous, etc.); 3) oxides of metals (lead, arsenic, selenium, magnesium, zinc, etc.); 4) alkaline gases (ammonia); 5) vapors of metals (mercury); 6) various organic gases and carcinogens (saturated and unsaturated hydrocarbons, phenol, carbon tetrachloride, etc.).

The composition of dust may include the most varied compounds formed during processing of raw materials of both acid and alkaline character, and also various salts, unburned coal particles, soot, etc.

The nature of the action of various acid gases on plants is apparently similar (Tomas, 1962; Nikolayevskiy, Kazantseva, 1965) and consists in modifying the physiological-biochemical processes as a result of acidification of the cell protoplasm. This causes an interruption of photosynthesis, an enhancement of the action of oxidizing enzymes, and the onset of photodynamic oxidations. The action of SO_2 on plants will be examined in more detail below, and also in a number of other articles.

Acid vapors cause the appearance of scorching or scalding on the surface of leaves. In this case, the veins of the leaves as well as the generative organs are damaged.

Like acid gases, ammonia penetrates the leaf mesophyll, and its injurious effect is due to the alkalinization of the cell environment.

The effect of mercury vapor (Kroker, 1950) and metal oxides on plants has been little studied, but it may be postulated that the mechanism and chemistry of their damage to the plants differs from that of acid gases.

Some metal oxides, for example magnesite dust (Kulagin, 1964 b), cause the death of woody plants not only because of plugging up the stomata and affecting the photosynthesis, but also as a result of a peculiar salinization of the soils, the interference with the mineral nutrition of the plants, and the reduction in the activity of useful microflora.

Hydrocarbons cause epinasty in plants (Nelyubov, 1900, 1910; Kroker, 1950) and other serious impairments of form development processes. A marked toxicity for plants is shown by many carcinogens (carbon tetrachloride, phenol). The nature of their action on plants is unknown.

Thus, the toxicity of compounds for plants depends on their chemical nature. In the action of these compounds one can distinguish (Nikoleyevskiy and Yatsenko, 1967) both a direct chemical action and a nonspecific action consisting in a change of the pH of the cell medium. This causes a change of the ionic equilibrium, as well as a change in the activity of the enzymes (their action becomes disordered), there is also a decrease in the stability of proteins and the biocolloids of the cytoplasm and the organelles of the cell decrease, and the character of plant metabolism is disturbed. The dealth of cells and tissues may be regarded as the result of advanced and irreversible processes of hydrolysis and photodynamic oxidations. The action of individual gases (chlorine) also has its specific aspects, apparently related to the characteristics of their direct chemical action.

It may be postulated that the nonspecific nature of action is characteristic of many other compounds (metal oxides, organic acids, phenol, etc.) that change the pH of the protoplasm. Gas mixtures and smog (Kroker, 1950; Tomas, 1962; Il'kun, 1968) are marked by a unique and specific character of action.

In the present paper it is practically impossible to describe all the toxic compounds, since their assortment increases each year, and the study of the influence of gases on plants and animals does not keep pace with the increase in air pollution.

Public health organizations have established permissible air pollution norms for many toxic compounds (Ryazanov, 1961 b; Uzhov, 1962). The maximum single permissible norm for pollution of air with sulfur dioxide is 0.5 mg/m^3, and the mean daily norm is 0.15 mg/m^3. They are respectively 0.03 mg/m^3 and 0.01 mg/m^3 for fluorine and 0.1 and 0.03 mg/m^3 for chlorine.

Since the mechanism of toxic action of many gases is different in autotrophic and heterotrophic organisms (Kroker, 1950), it may be postulated that for the former, the permissible air pollution norms of the All-Union State Sanitation Inspection will be unacceptable. Opinions on the permissible air pollution norms for plants are contradictory. V. A. Ryazanov (1961 b) holds that they are similar for animals and plants (SO_2), while other investigators

(Tomas, 1962; Ryabinin, 1962; Nikolayevskiy, Kazantseva, 1966) believe that the permissible air pollution norms for plants should be much lower than for animals.

While single norms of permissible air pollution have been established for man and animals, they cannot be single for plants of different sensitivity. Moreover, because of the change in the sensitivity of plants to gases in ontogenesis, the permissible norms even for a given species should be different at different stages of growth and development. The permissible air pollution norms for plants should be determined at the stages of heading and blooming, since at these stages the plants are least resistant to gases.

The fundamental solution to the problem of purity of atmospheric air, soil and water can be arrived at technologically, but even the most modern filters cannot completely eliminate the pollution of the environment. The development of new industries and new technological processes, the use of new types of raw materials, and the further development of motor transport will also, in the future, cause serious pollution of the biosphere by toxic compounds. On the other hand, the total utilization of waste at the majority of industrial plants has thus far proven economically unprofitable. Thus the biological method of purification of atmospheric air is of enormous importance. Green vegetation, soil, and the water surface of seas, which absorb the toxic compounds from air, prevent the poisoning of heterotrophs. According to the data of Zh. A. Medvedev and Ye. A. Fedorov (1956), in a closed space, up to 90% of sulfur dioxide is absorbed by plants in one hour, and the remainder by the soil and the surface of various objects.

Calculations show that the toxic compounds discharged into the atmosphere are enough to produce in the biosphere, for 23 years, a concentration above the maximum single permissible norms. If one considers that a substantial part of these compounds spreads through the atmosphere in the vicinity of the earth's surface (up to 1 km), the indicated concentration can be formed in the course of a single year. It is only because these compounds are utilized by plants, the soil, and the water surface of reservoirs that humanity is saved from self-poisoning, and thus life on earth is able to continue.

The concentrations of fluorine, chlorine and sulfur dioxide at a number of enterprises in the Ural (Yefimova, 1964; Timofeyeva, Sadilova, Kuperman, 1964; Sadilova, 1964) exceed the permissible norms set by the All-Union State Sanitation Institute by a factor of 5-10 or more.

General Characteristics of the Noxious Action of Acid Gases

Acid gases have a diverse influence on biogeocoenosis. Essentially, any of its components is exposed to the action of a new anthropogenic factor.

Even inanimate objects such as rocks, buildings and equipment are corroded by acid gases.

Acid compounds in the soil lead to the formation of salts that are readily washed out and to the loss of important basic elements (Ca, K and others) by the soil. Despite the incompetence of Wielera's soil decalcification theory (Krasinskiy, 1950), many researchers (Wentzel, 1954; Nikolayevskiy, 1964) have noted that gases reduce the fertility of soils, thus decreasing the viability and the gas resistance of plants. The noxious effect of acid compounds on the soil involves not only the washing out of important cations and a decrease of the soil absorbing complex, but also an impairment of the activity of the microflora and other organisms in the soil. We observed (Nikolayevskiy, 1964) at copper-smelting plants that the surface layer of imported fertile soil (up to 1 cm) under the influence of gases and pyrite dust in the course of 1-2 years becomes similar in agrochemical properties to the poisoned local soils. After swelling, seeds of many plants die on such soils (Nikolayevskiy and Suslova, in press). The absence of vegetation causes a considerable water and wind erosion of the soils, converting vast areas into industrial deserts.

Acid gases cause an impairment of growth (Krasinskiy, 1953; Gol'dberg, 1956; Lemke, 1961), a retardation or acceleration of plant development (Babushkin, 1955; Antipov, 1957, 1960; Yatsenko, Nikolayevskiy, Firger, and Suslova, 1968), a decrease of the yield (Kroker, 1950; Lemke, 1961; Thomas, 1962), the appearance on leaves of necroses differing in form and color depending on the types of plants and gases, and a change in the color of generative organs (Mirtov, 1961). Under the influence of SO_2, a change is observed in the color of flowers of dame's rocket and of ageratum. This phenomenon is caused by the acidification of the protoplasm under the influence of SO_2. Anthocyan changes its color under the influence of the pH of the medium from blue to pink and even red.

The poisoning of soils impairs root formation in plants (Ryabinin, 1962 a).

The shedding of leaves and needles in woody species (Krasinskiy, 1937, Nikolayevskiy, 1964) produces a sparse, openwork crown. In some species, a repeated change of foliage may lead to a disturbance in the correspondence of the morphophysiological rhythms to seasonal climatic conditions. Under the influence of gases, the plants' resistance to ecological factors decreases, and conversely, the latter may considerably influence the gas resistance of plants.

Different species of plants have different sensitivities to acid gases. For this reason, a change in the composition of phytocoenoses is observed in the vicinity of industrial enterprises: there is a disappearance of nonresistant species (blue grass, bedstraw, majanthemum, common chickweed, plantain, geranium, buttercups), while there is the preservation and a wider distribution of the resistant ones (Tatarian lettuce, toadflax, prostrate knotweed, meadow fescue, cinquefoil goosefoot, yarrow, shepherd's-purse, coltsfoot, horsetail). The quality of fodder grasses in meadows decreases. Pastures become unsuitable for cattle grazing.

In natural forest stands, one observes a decrease of the bonitet (by 1-2 classes) of the density of the stand, a decrease in the annual increment, a lowering of soil fertility, and an increase in the activity of pests (Jahnel, 1954; Lemke, 1961; Schneider and Sierpinski, 1968).

In the vicinity of aluminum plants, domestic cattle come down with fluorine cachexia because of the high fluorine content of the plants (Blagosklonov et al., 1967). Medical personnel have observed a decrease in the immunobiological reactivity of the organism in the juvenile population living in industrial areas (Navrotskiy,1960), resulting in a considerable spreading of infectious diseases. In animals (Battan, 1967), smog causes disturbances of the respiratory and cardiac activities. One of the causes of the widespread occurrence of cancer diseases today is thought to be the pollution of air with various carcinogenic agents.

Nature of the Noxious Effect of Acid Gases on Plants

Acid flue gases cause particularly serious and varied damage to green autotrophic organisms, since the assimilation of SO_2 instead of CO_2 quickly leads to the accumulation of toxic products in cells and to a serious impairment of many physiological-biochemical processes. The influence of acid gases on plants may be divided into direct action on the assimilative apparatus and indirect action via poisoning of the soils, deterioration of the conditions of mineral nutrition, and damaging effect on root systems (Nikolayevskiy and Yatsenko, 1968).

The degree of injury and hence damage because of gases depends on the toxicity of the gas, its concentration and duration of action, and the combination of weather-climatic conditions and species of plants. Most toxic for plants are F_2, Cl_2, SO_2, and smog (Tomas, 1962). V. Kroker (1950) gives the following sequence of gas toxicity for plants: $Cl_2 > SO_2 > NH_3 > HCN > H_2S$. On the other hand, their toxicity for animals and man is almost the opposite: $HCN > H_2S > Cl_2 > SO_2 > NH_3$. This distribution of the degree of toxicity of gases for plants and animals is undoubtedly due to the nature of their action on organisms. Compounds acting on the nervous and cardiac systems (HCN and H_2S) are more toxic for animals, whereas compounds decomposing the cell proteins and biocolloids and disturbing the autotrophic character of metabolism are more toxic for plants.

Vogl, Börtitz and Polster (1965) distinguish five degrees of injury to plants by sulfur dioxide depending on its concentration and the duration of the absorption of gas by the leaves: lack of injuries, latent injuries, or chronic, acute, and catastrophic injuries. Depending on the plants' sensitivity, under similar environmental and air pollution conditions, different species will have different injuries.

Under the influence of sulfur dioxide, necrosis blotches of different colors and shapes appear on plant leaves (Shabliovskiy, 1937). A characteristic feature is the fact that they are located on leaves between the veins, and in the case of grasses and conifers, at the tips of the leaves and needles. The color and shape of the necroses depend on the plant species, stages of growth and development, age of the leaves, and type of gas and its concentration in air. Young leaves have darker blotches and old leaves, lighter ones.

The fall of 4- to 5-year-old needles and frequently three-year-old needles is observed in coniferous species. Death of the latter (with the exception of the larch) in cities and at industrial enterprises is due not only to the injury of the needles, but also to a reduction of the assimilative surface and to carbohydrate deficiency (Nikolayevskiy, 1966). The increased survival rate of leaf-bearing species under these conditions is explained by the regeneration of the leaf apparatus.

The assimilative organs of plants are subject to greater injury, whereas the generative organs, stems, pedicles and veins of leaves, i.e., organs which do not participate appreciably in photosynthesis, are injured much less. Under the influence of acid gases, the yield of the vegetative mass and seeds decreases, and the seeds are frequently of lower quality and undersized.

Toxic gases and dust sharply reduce the productivity, quality, and density of plantings, and decrease the increment of trees in height and diameter (Ilyushin, 1953, 1961; Gol'dberg, 1956). American authors (Tomas, 1962) propose formulas for calculating the yield loss of agricultural crops on the basis of the concentrations of gases, time of their action, and vulnerability of leaves.

Acid gases and more rigorous microclimatic conditions prevailing in the areas of industrial plants cause an increase of xerophytization in the structure of leaves (Nikolayevskiy, 1966 b, 1967). Under industrial conditions, plants have smaller leaves and a larger thickness of the epidermis; the size of the cells and stomata decreases, and the number of stomata per mm^2 of leaf increases. The reduction of photosynthesis and formation of metabolites lead to a depression of the elongation stage and formation of small cells and leaves. On the other hand, xerophytization of leaves in plants frequently causes an increase in gas resistance (Isachenko, 1938; Nikolayevskiy, 1967).

Sulfur dioxide penetrates the leaf to a considerable extent through the stomata (Lotfild, 1921; Ivanov, 1936; Shabliovskiy, 1937; Krasinskiy, 1950; Jahnel, 1954; Nikolayevskiy, 1963; Kisser, 1968). Under the influence of SO_2, the regulation of the movement of stomata is disturbed, the degree of opening of the stomato decreases (Nikolayevskiy, 1964 b; Vogl, 1964), the intensity of motion of the protoplasm increases, and the permeability is enhanced (Morkovin, 1901). The functioning of the stomatal apparatus of plants accounts for their slight vulnerability at night, during dry spells, and in winter in coniferous species, since the stomato are closed at that time.

Initially, the injuries are concentrated in the spongy parenchyma near the stomata (Fortunatov, 1958). Acid gases cause the breakdown of lamellae, swelling and destruction of plastids, plasmolysis, and cell dehydration (Bredeman, 1933; Jahnel, 1954; Fortunatov, 1958; Il'kun et al., 1968). The cell nucleus is more resistant to gases than the plastids. In plants exposed to industrial conditions, the ventilation of the spongy parenchyma decreases, and sometimes one layer of palisade tissue falls out.

Using a tagged gas, Godzik (1968) found that woody plants differ markedly in their accumulation of $S^{35}O_2$. Autoradiography showed a nonuniformity in the absorption of the gas by the leaf. Sulfur dioxide concentrates in the leaf epidermis, in the coniferous needle endodermis, and in the water-conducting systems.

Acid gases cause serious disturbances of the water regime of plants. Under the influence of SO_2 transpiration first increases, then decreases (Morkovin, 1901; Kisser, 1968) as a result of an impairment of the water supply (Jahnel, 1954). Under the influence of chlorine (Kisser, 1968), the transpiration decreases at first, then increases.

In view of the specific character of the necroses formed on leaves (edges in dicotyledons, tips of needles in conifers and of leaves in grasses), it has been postulated that they are due to the water regime of the plants (Kisser, 1968; Nikolayevskiy and Suslova, in press). Toxic compounds move with the water current along the vessels and toward the edges and tips of the needles and leaves, and concentrate, reaching lethal doses.

Acid gases cause the interruption of photosynthesis in plants (Ivanov, 1936; Thomas and Hill, 1937; Jahnel, 1954). The degree of influence of gases on photosynthesis and the nature of the aftereffect depend on the concentration of the gases. The action of SO_2 disturbs the synthesis of sugars; pigments, proteins, polysaccharides, and vitamins break down (Krasinskiy, 1950; Jahnel, 1954; Holte, 1958; Fortunatov, 1958).

Particularly contradictory are the views held by researchers concerning the influence of acid gases on plant respiration: some (Zheleznova-Kaminskaya, 1953; Ilyushin, 1953; Ryabinin, 1962 b) postulate that respiration and the respiratory quotient increase, while others (Thomas and Hill, 1937; Krasinskiy, 1950) hold that SO_2 has no appreciable influence on plant respiration. In our view, the contradiction is due to the lack of reliable experiments. In the majority of cases, the respiration was studied after the lapse of a considerable period of time since the time of action of SO_2. Respiration, as a process most labile and sensitive to changes in the environment, must undoubtedly undergo some profound changes. We established (Nikolayevskiy, 1968) that SO_2 alters the chemistry of respiration in plants. In resistant species (summer-cypress, Eastern poplar, box elder), SO_2 enhances the role of the pentose monophosphate oxidation route, whereas in nonresistant species (European white birch, balsam poplar), the role of the Krebs cycle in respiration is enhanced. In view of the major adaptive significance of respiration and its role in the immunity of plants (Rubin, Artsikhovskaya, 1960; Turkova, 1963; Rubin, Ladygina, 1966) it would be difficult to represent it as neutral toward acid gases.

Under the influence of acid gases, the activity of enolase, phosphatase, amylase, and catalase is reduced (Krasinskiy, 1950; Fortunatov, 1958; Nikolayevskiy, Suslova, 1968), while the activity of peroxidase and polyphenol oxidase is increased. We were the first to confirm experimentally (Nikolayevskiy and Miroshnikova, 1968) K. Noack's theory (1920, 1924) concerning the formation of photodynamic oxidation processes under the influence of SO_2.

Sulfur dioxide causes a sharp increase in oxidation processes in both etiolated and green plants, and only concentrated gas causes inhibition of luminescence and respiration. Thus, slight SO_2 concentrations cause an increase in respiration and ultrafaint luminescence of plants and an increase in the activity of oxidizing enzymes. High SO_2 concentrations cause a depression of luminescence, discontinuation of respiration, and a rapid death.

Acid gases and poisoned soils at industrial plants cause a loss of germinating power in seeds and a disturbance of the rhythms of growth and development. Usually, the initial stages of development of plants are delayed (in woody plants - the swelling of buds, in forage grasses - sprouts, third leaf and tillering), and the subsequent stages are accelerated (Yatsenko et al. 1968; Suslova and Nikolayevskiy, 1968; Firger and Nikolayevskiy, 1968). The duration of the vegetative stage is shortened in some plants (Antipov, 1957), and in others increases as a result of second and sometimes multiple leaf formation. The decreases in the yielding capacity of forage grasses is directly related to the degree of influence of gases.

Theories of the Gas Resistance of Plants

By gas resistance (Krasinskiy, 1950), the majority of investigators mean the ability of plants acted upon by gases to preserve their growth, development, and ornamental properties.

Many authors have proposed different hypotheses regarding the causes of the vulnerability and gas resistance of plants. Individual physiological or biochemical indices or processes are very frequently used in the explanations. At the same time, the diversity and complexity of the mechanism and chemistry of the effect of acid gases on plants are ignored. This effect is due to the complexity of the constitution of living matter (plants) and the marked qualitative diversity between different species as well as within a species.

The compilation of assortments of gas-resistant plants should have as its theoretical basis an exact knowledge of the physiological-biochemical processes responsible for the differences in the vulnerability and gas resistance of plants. It is particularly interesting and important to know the chemistry of conversion of sulfur dioxide in plants and its influence on the metabolism, the oxidation-reduction processes, and the stability of cell proteins and biocolloids.

Haselgof and Lindau (1903) held the cause of necroses and death of plants to be the interaction with carbohydrates in the leaves, but it was noted that the stronger plants are injured in the morning, when the leaves contain less carbohydrates.

Schreder, Reus and Wieler (1912) held that gases act on plants indirectly, via the soil. They identified the gas resistance with the ability to grow on poisoned soils. We have established (Nikolayevskiy and Suslova, in press) that on poisoned soils, even nonresistant species can germinate, whereas resistant ones may die. Consequently, the survival rate of plants must not be identified with their gas resistance. On the other hand, despite a considerable indirect damage done by poisoned soils, the cause of injury and death of the plants in this case appears to be different.

K. Noack (1920) was the first to use the laws of photochemistry in connection with gas resistance. Sulfur dioxide blocks photosynthesis, but it does not affect the binding of luminous energy by pigments. The latter gives rise to photodynamic oxidation processes that result in the formation of burns on leaves.

Dorris (quoted by Tomas, 1962) held that SO_2 causes the oxidation of chlorophyll. The formation of pheophytin leads to the death of the leaf tissue.

According to Bleasdale (1932), sulfur dioxide disturbs the equilibrium in the content of the SO_4 anion and of sulfhydryl groups in plants. This leads to a disturbance of metabolism and to leaf injury.

Nemec (1958) held that the accumulation of sulfur dioxide by leaves promotes the absorption of cations of toxic metals (Zn, Al, Cu, Pb, As, etc.) from the soil. The latter cause the conversion of chlorophyll into pheophytin and the discontinuation of photosynthesis. The death of plants is the result of both poisoning by these compounds and carbohydrate deficiency.

A major contribution to the development of the gas resistance theory was made by N. P. Krasinskiy (1937, 1939, 1950) and his students (Knyazeva, 1950; Guseva, 1950, and others). He proposed that gas resistance be divided into three arbitrary types: 1 - biological resistance consisting in the ability of plants to rapidly regenerate the damaged foliage, a feature characteristic of rapidly growing woody species; 2 - anatomical-morphological resistance, because of leaf structure characteristics that slow down the rate of gaseous exchange and accumulation of toxic gases; 3 - physiological-biochemical resistance connected with the physiological-biochemical characteristics of plants. Yu. Z. Kulagin (1968) distinguishes a fourth type of resistance - anabiotic gas resistance. In the state of anabiosis, for example, coniferous species are not damaged by gases in winter.

N. P. Krasinskiy (1950) showed that plants containing a large quantity of readily oxidizable organic substances are more extensively damaged as a result of photodynamic oxidation processes. He used this to confirm K. Noack's hypothesis (1920). Krasinskiy (1950) ascribed a major importance in gas resistance to the reducing properties of the cell content and to the chemistry of metabolism. He considered gas resistance to be a systematic index of the species, genera, and families of plants. The cruciferae family were found to be the most resistant, and legumes, the least resistant. V. M. Babkina (1968) holds that evolutionarily young species are more resistant than the old, ancient ones. Gurkal (1959) attributes this to differences in the nature of metabolism. Plants that are evolutionarily progressive have an unspecialized metabolism (a greater variety of products of metabolism) and are thus better able to tolerate the action of SO_2. Ancient species have a specialized type of metabolism (Blagoveshchenskiy, 1950) and are therefore less resistant to gases.

The available literature data and reviews (Krasinskiy, 1950; Kroker, 1950; Tomas, 1962; Jahnel, 1954) and also the results of our studies make it possible to state some preliminary views on the mechanism by which plants are injured by acid gases and on the causes of differences in the gas resistance of plants.

The degree of injury to plants by sulfur dioxide depends on the rate of absorption of the gas. Injuries in plants occur after a lethal level of sulfur compounds has been reached (Ivanov, 1936; Krotova, 1957; Jahnel, 1954). The anatomical-morphological structure of leaves (Knyazeva, 1950) and the function of the stomatal apparatus (Nikolayevskiy, 1963, 1964 b), which promote an increase in the intensity of gas exchange, are at the same time the cause of the high vulnerability of plants to damage from sulfur dioxide. The high rate of gaseous exchange in woody plants is provided by the high degree of aeration of the spongy parenchyma of the leaf (Knyazeva, 1950; Nikolayevskiy, 1966 b, 1967) the lack of distinct mechanical coatings (cuticle, hairs), a long period of open stomata in the course of 24 hours, a ratio of the height of palisade tissue to that of spongy tissue of less than one, and the presence of stomata on both sides of the leaf.

In contrast to literature data (Knyazeva, 1950; Fortunatov, 1958) we observed a statistically significant inverse correlation between the quantity of stomata and the vulnerability (Nikolayevskiy, 1966 b, 1967; Nikolayevskiy and Firger, in press). A large number of fine stomata and a high degree of regulation of their movements indicate an increased ecological flexibility of gas-resistant plants. The leaves of gas-resistant woody plants (box elder, European spindle tree, snowberry) are subject to a whole series of characteristics which slow down the rate of gaseous exchange, namely, the presence of pubescensce or additional coatings (silverberry), a lesser aeration of spongy parenchyma, the magnitude of the ratio hn/hr, a decrease in the degree of opening of the stomata during the day.

As established by Ye. I. Knyazeva (1950) and us, the role of the anatomical-morphological structure of leaves in the gas resistance of plants makes it necessary to postulate that differences in gas resistance are due to different rates of absorption of acid gases. The same conclusion was reached by Tomas, (1962).

According to the data of Krotova (1953), the lethal level of sulfur accumulation by leaves of woody plants is lower in gas-resistant species than in nonresistant ones (maple 0.3-0.4%, poplar, dogwood, ash 0.75-0.9%). In forage grasses (Nikolayevskiy and Suslova, in press), in contrast, the lethal level of sulfur accumulation is frequently higher in the more resistant species. This characteristic of plants serves as the basis for selecting species with an increased gas-absorption capacity (Kulagin, 1968; Getko, 1968) for the purpose of making possible a greater sanitary-hygienic role of plantings. On the other hand, one can postulate a deeper and theoretically important relationship between the vulnerability of plants and the intensity of photosynthesis and respiration, metabolism, and direction of biochemical processes.

Some researchers (Krotova, 1953) have assumed that resistant plants are characterized by a higher intensity of photosynthesis. First, they proceeded from the fact of the low gas resistance of coniferous woody species, which have (Ivanov, 1936) a low photosynthesis, and, second, they assumed that the products of photosynthesis (carbohydrates) are utilized by the plant for detoxicating* the sulfur compounds. Our studies (Nikolayevskiy, 1963, 1967) showed a direct correlation between the vulnerability and the rate of photosynthesis ($r = 0.79$). Resistant species (box elder) are characterized by a decreased rate of photosynthesis, and nonresistant species (European white birch, Manchurian walnut, etc.) - by a faster photosynthesis rate.

Subsequently, the cause of the low gas resistance of coniferous species to the action of gases was cleared up (Nikolayevskiy, 1966 a). It was found that the coniferous species were more resistant than the leaf-bearing ones to a single action of even high SO_2 concentrations, with the exception of the genus Larix. Their low survival rate in cities is because the coniferous needles have a long lifespan and hence are exposed to the action of gases for a longer time. A reduction of the assimilative surface (because of shedding of the old coniferous needles) leads to the death of the plants as a result of carbohydrate starvation.

The dependence of the gas resistance of plants on the intensity of gaseous exchange is confirmed, on the one hand, by the anatomical-morphological structure of the assimilative organs of the plants, and on the other hand, by examples of reduction of plant vulnerability in the shade, the absence of injury at night and during the winter season, and also the absence of injuries in organs and parts not taking any appreciable part in photosynthesis (petioles, leaf veins, young shoots, and the reproductive organs). The low intensity of photosynthesis explains the high resistance of succulents (echeveria, sedum). According to literature data (Brilliant, 1951), the intensity of photosynthesis in the cruciferae is 1.5 times lower than in legumes. Tomas (1962) and Il'kun (1968) also hold that differences in the gas resistance of plants are primarily due to differences in the rates of absorption of sulfur dioxide.

An important role in gas resistance is played by the direction of the physiological-biochemical processes. N. P. Krasinskiy (1950) showed that resistant plants are characterized by increased reducing properties of the protoplasm and a higher content of glutathione. V. A. Guseva (1950) observed that resistant plants are characterized by a lower oxidation-reduction potential (ORP) and aerobicity index rH_2. Our studies (Nikolayevskiy, 1965 a) confirmed Guseva's data (1950). In addition, a direct relationship was observed between the vulnerability of plants to sulfur dioxide and the content of ascorbic acid in the leaves. It is well known that a high ascorbic acid content correlates in plants with a high oxidation activity (Rubin, Spiridonova, 1940). According to the data of L. Michaelis (1936) and T. F. Lupareva

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* [Translator's note: "intoxicating" in Russian original.]

(1958), an equality of the oxidation and reduction processes in plants is observed when index rH_2 = 13-14. For gas-resistant woody plants, rH_2 is found to be 13-15, and for nonresistant ones, 16-20. Hence, resistant plants are characterized by a lower intensity of photosynthesis, a low ascorbic acid content, and a relatively high activity of reduction processes. Experiments (Nikolayevskiy and Suslova, 1968) established that under the influence of SO_2 and H_2SO_4 the resistant plants show, at first, an increase of the reducing properties, while in the case of nonresistant species one finds an increase in the oxidizing properties of the protoplasm. Krasinskiy's hypothesis (1950) concerning the role of oxidizable substances in gas resistance requires an experimental biochemical verification. Many physiologists do not accept his "oxidizability" index because of the roughness of the determination and biochemical vagueness.

A study of the content of substances oxidizable with 0.1 N $KMnO_4$ in leaves by Krasinskiy's method (1950) confirmed his conclusions concerning the dependence of gas resistance on the quantity of oxidizable substances. The correlation coefficient for 47 leaf-bearing woody plants was 0.54 at $\frac{r}{m_r} = 7.7 > 3$. It was postulated (Nikolayevskiy, 1963) that the content of oxidizable substances in leaves is related to the intensity and direction of the physiological processes. It thus becomes possible to understand, on the one hand, the causes of the diverse gas resistance of plants (differences in photosynthesis rates) and, on the other hand, the causes of the relationship between the vulnerability of plants and the quantity of substances in leaves oxidizable by potassium permanganate. Species differences in the intensity of photosynthesis in plants are of course related to the activity of oxidation-reduction enzymes. It may be assumed that the activity of photodynamic oxidations in plants under the influence of SO_2 will depend on the activity of the oxidizing enzymes of plants.

Of major importance for the gas resistance of plants should be the nature of metabolism (Nemec, 1957). Gurkal (1959) observed that resistant forms of Norway spruce contained much higher amounts of α-pinene in their needles. The positive role of pentose phosphate type oxidation in the drought resistance (Abrarov and Petinov, 1964) and immunity (Rubin and Zeleneva, 1964) of plants is explained by the formation of compounds with increased reducing properties. Apparently, the same role is played by the apotomic oxidation route in the respiration of gas resistant plants under the influence of SO_2 (Nikolayevskiy, 1968).

The chemistry of transformation of sulfur dioxide in plant leaves is complex and thus far unclear, since SO_2 may be simultaneously an oxidant and a reductant. It is possible that the nature of the transformation of SO_2 and its influence on the metabolism of plants of different resistances will be different. It is thought (Kroker, 1950; Yang and Mou, 1961; Tomas, 1962) that SO_2 is oxidized to the sulfate and is partially tied up by organic compounds. As a result, the toxicity of SO_2 decreases by a factor of 30. Simultaneously with the oxidation of sulfite, sulfurous and sulfuric acids are formed, acidifying the protoplasm (Krasinskiy, 1950).

In the case of sulfur deficiency in the soil (Kroker, 1950), the sulfur is rapidly included in the composition of amino acids and proteins in reduced form. This accounts for the beneficial effect of SO_2 on plants in areas of the USA with a low sulfur content of the soil.

The reduction of sulfate proceeds in light (Doman, 1957) through oxidation of the carbohydrates (Sabinin, 1955; Kaliniyevich, 1959). Nemec (1957) and Tomas (1962) emphasize that carbohydrates also have a beneficial influence on the gas resistance of plants.

Thomas and Hill (1937) observed that sulfate is excreted into the soil by the root systems of plants that have been exposed to SO_2. It is possible that this is the way in which plants can regulate the sulfur content of tissues and avoid toxic concentrations.

A study of the water regime showed that woody plants resistant to SO_2 (box elder, elder, etc.) are characterized by an increased water content and water-holding capacity, a low concentration of cell content, and a moderate content of bound water (Nikolayevskiy, 1965 b). For plants not resistant to sulfur dioxide (white birch, Siberian crabapple, etc.), the opposite is true.

A great similarity is frequently observed in the action of certain acid gases on green plants. Rohmeder and Schönborn (1965) note that plants resistant to SO_2 display a high resistance to fluorine. This was also observed by us (Nikolayevskiy and Yatsenko, 1968; Firger and Nikolayevskiy, 1968) at the Perm' Chemical Plant in 1966-1967.

According to the studies made by Ye. N. Kazantseva (1965), forage and herbaceous ornamental plants resistant to fluorine are characterized by similar anatomical-morphological and physiological characteristics, as are also the SO_2-resistant woody plants. This appears to be a manifestation of the above-indicated nonspecificity of the action of acid gases on plants, leading to a disturbance of the dark reactions of photosynthesis and to the appearance of photodynamic oxidation processes in light (Nikolayevskiy and Kazantseva, 1966).

The survival rate of plants under industrial conditions is determined not only by their gas resistance, but also by the action of other ecological factors: frosts, droughts, or soil salinization. Ilyushin (1953), Krotova (1957), Nikolayevskiy (1964), and Kulagin (1965) hold that drought- and frost-resistant plants also display a higher gas resistance. The drought resistance of the silverberry is explained by the presence of special umbellate excrescences of the cuticle which cover entirely both surfaces of the leaf and protect it from overheating; they also decrease the evaporation of moisture. The high resistance of the silverberry to SO_2 and F is explained by the fact that the excrescences of the cuticle slow down the rate of gaseous exchange and absorption of toxic compounds.

Of interest is the fact that the water-holding capacity is a universal indicator of the resistance of plants to various extreme factors (low temperatures, droughts, gases). Hence, the resistance of plants requires the preservation of the structure and functions of the proteins and biocolloids of the protoplasm and organelles of the cell.

In our view (Nikolayevskiy, 1965 a), the striking analogy in the resistance of plants of three families to different factors is not accidental. N. P. Krasinskiy (1950) observed a high resistance of the cruciferae and low resistance of legumes to SO_2. Cereals occupy an intermediate position in their resistance to SO_2. The same was observed in the case of their tolerance of ionizing radiations (Vasil'yev, 1962; Preobrazhenskaya, and Timofeyev-Resovskiy, 1962).

The sensitivity to ionizing radiation is associated with a high intensity of vital processes (Vasil'yev, 1962). The analogy in the behavior of plants toward the action of different factors may be attributed to the fact that the gas and radiation resistance is based on the intensity and direction of the physiological-biochemical processes. At the basis of the biochemical processes of injury to plants by x rays (Dubinin, 1961) and gases (K. Noack, 1920; Krasinskiy, 1950) lies a disturbance of the processes of accumulation of luminous energy and photosynthesis, and the appearance of similar photodynamic oxidations.

Yu. Z. Kulagin (1965, 1966 a) successfully developed an ecological concept of gas resistance, whereby the degree of plant resistance is determined, in addition to everything else, by the presence or absence of critical periods. If the critical period in plants happends to coincide with the action of a gas, even relatively resistant species may die, and conversely, nonresistant plants which have excaped injury during critical periods may survive.

Experience in compiling assortments of gas-resistant plants (Nikolayevskiy and Kazantseva, 1965; Nikolayevskiy and Firger, 1969, in press) and their comparisons with similar lists of other authors (Shabliovskiy, 1937; Isachenko, 1938; Krasinskiy and Knyazeva, 1950; Zheleznova-Kaminskaya, 1953; Deroyan, 1957; Kuntsevich and Turchinskaya, 1957; Bulgakov, 1958; Vanifatov, 1958; Podzorov, 1961; Gayevaya, 1962; Ryabinin, 1962; Sitnikova, 1966; V. M. Babkina, 1968) show that it is impossible to obtain universal lists. The physicogeographical conditions of individual regions may exert a substantial influence on the anatomical-morphological and physiological-biochemical characteristics and gas resistance of plants. A considerable geographical variability of gas resistance is observed in the box elder. Under the conditions of the Ural and Moscow regions, the box elder is considered to be a gas-resistant species, but in Karaganda, Transcaucasia, the Donets Basin and Dnepropetrovsk, it was found to be nonresistant. These areas differ in their moisture regime. Drought conditions (Karaganda, Dnepropetrovsk) complicate the water regime of plants and decrease the resistance of the protoplasm proteins, causing a decrease in gas resistance.

The literature gives indications of the important role of mineral nutrition in the gas resistance of plants (Nemec, 1957; Kazantseva, 1965; Kisser, 1968; Yatsenko et al., 1968), and of the moisture regime (Jahnel, 1954), illumination, and temperature (Kroker, 1950; Krasinskiy, 1950).* A given combination of ecological conditions may foster an increase of the gas concentration in the ground layer of air. In addition, by reducing the general vital capacity of plants, frosts and high temperatures may bring about a high injury rate even in the case of low gas concentrations.

Thus, the resistance of plants to acid gases depends on the following conditions: (a) combination of the complex of ecological factors at the time of the action of gases, (b) biological characteristics of the species and their ecological flexibility, (c) stages of plant growth and development, (d) anatomical-morphological structure of the leaves, (e) intensity of gaseous exchange, (f) stability of the proteins and biocolloids of the cell, (g) degree of disorganization caused by the gases in metabolism and enzyme activity, (h) nature and intensity of photodynamic oxidation processes, and (i) the buffering capacity of the cell content and other factors.

For certain specific gases and geographical areas, many authors recommend different assortments of gas resistant plants for use around industrial enterprises. More than 20 lists of recommended plants have been proposed in the USSR. The gas resistance criteria used are (a) the plant vulnerability index (Krasinskiy, 1937, 1950; Antipov, 1959), (b) the survival rate under unfavorable conditions (Bulgakov, 1958), (c) the quantity of oxidizable substances in the leaves (Vanifatov, 1958; Antipov, 1968), and (d) the effect of gases on the physiological and growth processes of plants (Sitnikova, 1964, 1966).

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* Some of the other papers presented in this volume, which deal with studies on the gas resistance of plants in relation to the problems of mineral nutrition, metabolism of C^{14} carbon compounds under the influence of SO_2, and influence of the gas on the pigment systems and ultrafaint luminescence of plants, may serve as a supplement to the survey reported in this paper.

Conclusion

The present study gives a survey of the principal advances in research on the gas resistance of plants in the USSR and in the countries of Europe and America. In a survey of this kind it is practically impossible to give a detailed review of all the published studies dealing with this topic.* We have attempted to mention the key points that are conducive in some measure to the elucidation of the causes of plant vulnerability and gas resistance. Since the beginning of these investigations, important data - both from the theoretical and the practical point of view - have been obtained which are conducive to the clarification of the causes of the diverse resistance of plants. Thus, the influence of toxic compounds on the anatomical-morphological structure of leaves and the physiological-biochemical characteristics of plants have been studied. Also, the species of plants resistant to various compounds in different physico-geographical zones have been ascertained. Many investigators have made a serious contribution to the development of the theory of plant resistance to acid gases. In several countries (U.S.A., USSR, Poland), investigators have undertaken detailed studies of the chemistry of injuries to plants by acid gases as well as of the chemical mechanism of transformation of SO_2 in plants and its influence on the metabolism of carbon compounds with the aid of modern isotopic methods of analysis using $S^{35}O_2$ and C^{14}. Major advances have been made in the study of the resistance of plants to sulfur dioxide, while at the same time insufficient attention has been given to the study of the resistance of plants to chlorine, hydrogen sulfide, hydrocarbons, carcinogenic compounds and to the other ingredients which pollute the atmospheric air. There have been practically no investigations into the influence of the chemical compounds on the microflora of soils.

Of major importance for a successful diagnosis and study of the gas resistance of plants is the establishment of direct indicators characterizing the degree of plant resistance. We have given considerable attention to the development of methods for studying the gas resistance of plants. Two methodical studies have been especially devoted to this problem.

Research carried out in the last two years has shown that under the influence of fertilizers, forage grasses do not always clearly display the relationship between the change in the content of ascorbic acid, oxidizable substances, water-holding capacity, and gas resistance.** Apparently, these indicators do not reflect the direct relationship to the gas resistance, but are indirect, describing the intensity of physiological-biochemical processes and the stability of protoplasmic biocolloids. This once more underscores the necessity of studying the mechanism and chemistry of injury to plants by gases and the causes of the diverse gas resistance of plants. The establishment of direct indicators of gas resistance will aid in a correct appraisal of the resistance of individual plant species.

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* Some of the remaining studies of this volume supplement the present paper to some extent.

** See the paper of Yatsenko and Nikolayevskiy in this volume.

The present day status of the problem of plant gas resistance in the USSR and other countries (Transactions of the 6th International Conference on the Problem of "Effect of Smoke Pollution of Air on Forests," 1968) and the lack of a unified, generally accepted theory of plant gas resistance point up the urgent necessity of:

1 - Studying the physiological-biochemical bases of the gas resistance of plants;

2 - Studying the chemistry of transformation of toxic compounds in plants and the mechanism of their detoxication*;

3 - Developing methods of increasing the gas resistance of plants;

4 - Studying the sanitary-hygienic role of plants.

On the basis of our studies, to characterize the gas resistance, we can recommend the determination of certain indicators correlating with the resistance:

1 - Anatomical-morphological structure of leaves (number of stomata, thickness of epidermis, aeration of spongy tissue, daily dynamics of the movement of stomata), which characterize the rate of absorption of acid gases;

2 - Ascorbic acid content, which characterizes the rate of metabolism and the activity of oxidation processes;

3 - Water-holding capacity, characterizing the hydrophily and resistance of proteins and biocolloids of the protoplasm;

4 - Quantity of oxidizable substances in the leaves, using N. P. Krasinskiy's method (1950);

5 - Vulnerability of plants to gases under both industrial and experimental conditions;

6 - Determination of the lethal and sublethal doses of absorption of sulfur dioxide by means of a tagged gas ($S^{35}O_2$).

We have developed a new method of determining the aeration of the spongy parenchyma of leaves by means of vacuum infiltration.

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* [Translator's note: "intoxication" in the Russian original.]

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EFFECT OF MINERAL NUTRITION ON THE GAS RESISTANCE OF FORAGE GRASSES

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From Akademiya Nauk Ukrainskoy SSR. Tsentral'nyy respublikanskiy botanicheskiy sad. Donetskiy botanicheskiy sad. Materialy Pervoy Ukrainskoy konferentsii "Rasteniya i promyshlennaya sreda". Izdatel'stvo "Naukova dumka", Kiev, p. 88-94, (1968).

A successful planting of greenery on the grounds of industrial enterprises discharging noxious gases is not dependent solely on sound selection of an assortment of gas-resistant plants. Of late, research men and practical gardeners have come to the conclusion that it is necessary to develop special agro-technical methods of fertilizer application in order to produce more viable and resistant plantings and compositions (Guseva, 1950; Krasinskiy, 1950; Wentzel, 1959; Materna, 1963). Traditional agro-technical methods of plant cultivation, borrowed from the practices of farming and forestry, have proven relatively unsuccessful and inadequate. The highly unfavorable ecological conditions for plants at industrial sites make it necessary to test old methods (Guseva, 1950; Materna, 1963) as well as, in the main, new agro-technical methods (Bobko and Fortunatov, 1958) and ways of growing plants and increasing their gas resistance.

In 1967, we attempted to use a field method for studying the influence of the elements of mineral nutrition on the growth, development and gas resistance of forage grasses (a) under the conditions prevailing at two industrial enterprises (a chemical plant emitting SO_2, F, HF, and nitrogen oxides, and a nonferrous metallurgical plant discharging Cl_2 and SO_2) and (b) under experimental conditions at the Botanical Garden of Perm University. We used an 8-treatment experimental scheme (control, N, P, K, NP, NK, PK, NPK). The resistant species chosen for this investigation was meadow fescue (Festuca pratensis Huds) and the non-resistent species chosen were timothy grass (Phleum pratense L.).

Prior to sowing, fertilizers were applied to the plots in the following proportions: K - 9g, N - 4g, and P - 6g per 1 m^2. At the Botanical Garden, the plants (10 in each test glass) were fumigated with sulfur dioxide in chambers (SO_2 concentration from 0.03% to 0.4% by volume, 1 hour). The vulnerability was determined by linear measurement of necroses in the second leaf (from the top) in ten replications. At the end of the summer, the yield (plant height and number of leaves) was calculated for each treatment. In addition, foliar nutrition (fertilizer spray applications) tests were conducted at the Botanical Garden to determine the effect of the same fertilizers and of certain physiologically active substances on the gas resistance of the plants. Since the effect of fertilizers in a field experiment may be levelled by the action of other factors, a periodic dressing of the plants with fertilizers was carried out at the Botanical Garden according to the same scheme and norms, starting on 12 July and their influence on the vulnerability and on certain biochemical characteristics of the plants (quantity of substances undergoing oxidation and of ascorbic acid, oxidation-reduction potential, and content of organic acids) was determined.

The studies showed that in the course of the growing period, the gas resistance is maximum at the stage of emergence of the seedlings and at the stage of 3 leaves, then decreases, and slightly increases at the end of August. This is apparently due to the intensification and character of metabolism in the middle of summer in the fescue and in the stages of booting, heading, and blossoming of timothy grass. It is very likely that the differences of gas resistance between meadow fescue and timothy grass are due to the biological characteristics of the growth and development of these species. During the first year, the fescue ends its growth with the tillering stage and blossoming takes place in the second year, whereas the timothy grass completes during the first year its full life cycle. Because of an intensification of metabolism, the gas resistance of timothy grass is sharply reduced during the heading and blossoming stages.

In meadow fescue at the chemical plant, the course of the developmental stages lags 1-3 days behind the Botanical Garden plants for the emergence of seedlings stage; 6-9 days for the third-leaf stage, and 9-12 days for the tillering stage. Thus, under the influence of acid gases and poisoned soils, the growth and development of the fescue at the chemical plant are retarded, and this lag increases at each stage. In timothy grass, a lag also takes place during the first three stages of growth and development (emergence 1-2 days, third leaf 5-9 days, tillering 5-9 days). However, a substantial acceleration of development (6-12 days) is observed as early as during the booting stage. The acceleration of development in timothy grass is preserved during the heading stage in treatments N, P, K, and NK. A retardation of development recurs in the remaining treatments and stages.

Whereas in the Botanical Garden, timothy grass passed through all the growth-development stages up to the ripening of seed in all the treatments of the experiment, such was not the case at the chemical plant where timothy completed its life cycle only in treatments N, P, K, and NK. In the remaining treatments it did not go on to the formation of the reproductive organs. Hence, as in the case of the meadow fescue, under the influence of acid gases and poisoned soils, a retardation of development is observed in timothy grass during the first three stages near the chemical plant, followed by a substantial acceleration of its development during subsequent stages. In the control timothy plants, growing near the chemical plant, the life cycle cannot be completed in a one-year period. In treatments with fertilizers, the plants also did not reach the blossoming stage. Nitrogen, phosphorus, potassium, and nitrogen-potassium cause an acceleration of the growth and development at the heading stage and the termination of the life cycle of timothy grass in one year.

Table 1

Influence of Mineral Nutrition on the Gas Resistance of Forage Grasses

Treatments	Vulnerability of Plant in Percent of Control					
	Meadow fescue			Timothy grass		
	Botanical garden	Chemical plant	Metallurgical plant	Botanical garden	Chemical plant	Metallurgical plant
Control	I00	100	I00	I00	I00	I00
N	II3	I00	64,3	90	9I,5	I05,2
P	I09	I25	I0I	I0I	I09	I24,0
K	I35	96	92	83,3	I28	III,2
N_p	I09	97,7	68,8	67	62	II4,2
Nk	89	I07	80,6	I00	I0I	I08
pK	I32	I29	I00,2	I03	96	76,5
N_{pk}	I54,7	128	6I,0	I20	I0I	I33,0

It was found (Table 1) that the species in the Botanical Garden differed more markedly in gas resistance, whereas at the chemical plant the differences were reduced, and at the metallurgical plant the resistance of the plants in the control treatment was similar. These characteristics may be explained by differences in the composition of the gases acting on the plants, in weather and climatic conditions, and in the degree of poisoning of the soils. Particularly unfavorable in this respect were the conditions prevailing at the metallurgical plant.

According to average data for the growth period (Table 1), a favorable effect on the gas resistance of meadow fescue in the Botanical Garden was that of nitrogen-potassium, and in the case of timothy grass, those of nitrogen, potassium, and nitrogen-phosphorus. At the chemical plant, an increase of gas resistance was observed in meadow fescue in the potassium and NP treatments, and in the case of timothy with the N, NP and PK treatments. At the metallurgical plant, the vulnerability of fescue decreased in the N, K, NP, NK, and NPK treatments, and in the case of timothy grass, only in the PK treatment. Thus, mineral fertilizers can be used to control the gas resistance of forage grasses. Different elements as well as different mixed fertilizer treatments, produce a positive effect on plant resistance. This depends on the biological characteristics of the species, on changes in the requirements of the plants for mineral nutrition and ontogenesis, and on the influence exerted on the plants by the poisoned soil of the industrial areas. Analyses showed that the soils near the chemical plant have a substantially reduced content of mobile forms of nitrogen, phosphorus and potassium.

An experimental study of the influence of mineral fertilizers on gas resistance as determined from the growth and development stages showed that in meadow fescue, even in the course of a single stage (tillering), a succession of the positively acting nutrient elements is observed in different calendar periods, i.e., June-July-August. In timothy grass, the same phenomenon can be observed in accordance with the growth and developmental stages. In meadow fescue, depending on the calendar periods, N, P, K, NP, and NK were found to have a positive effect on the gas resistance, and in the case of timothy grass, NP, N, K, and NK. The succession of nutrient elements having a positive effect on gas resistance in plant ontogenesis is completely regular. The mineral requirements of plants are a function of their growth and development and of the biological characteristics of the species.

The positive effect of fertilizers on plant growth (height of shoots, length of leaves) also changes in plant ontogenesis. In the fescue, at the beginning of summer, an increase in leaf size was observed in all the treatments. In the middle of summer, the fertilizers caused a decrease in stem growth and an increase in leaf growth, whereas at the beginning of August the fertilizers decreased the leaf growth, and in the middle of August the positive effect of fertilizers on the growth of the plants was manifested again.

In timothy grass at the beginning of summer, almost all the treatments produced a positive effect on the growth of the plants. This was followed by a depression of shoot growth and an enhancement of leaf growth in treatments N, P, and K.

In gas resistance of fescue in the first year of life (tillering), the most important role is played by nitrogen (Botanical Garden) and potassium (chemical plant), and by nitrogen in the case of timothy grass. The positive role played by nitrogen in the gas resistance and also in the growth and development of plants is explained by the important part which it plays in their protein metabolism.

Experiments with foliar nutrition showed that the gas resistance in fescue is increased by potassium, and in timothy grass by N, NK, and K. A positive effect in fescue was produced with potassium ferricyanide and citric and malic acids; and in timothy grass, in addition, by oxalic acid, NaOH, boron, molybdenum, and hydroquinone. A negative effect was produced in both species by P, PK, NPK, $CaCO_3$, $ZnSO_4$, $MgSO_4$, $FeSO_4$, $KMnO_4$, and H_2SO_4.

The positive influence of organic acids on the gas resistance of forage plants can be explained by their important role in plant respiration (tricarboxylic acid cycle). The adverse effect of sulfates and H_2SO_4 on plants can be explained by the additional negative influence of the SO_4 anion.

Potassium permanganate is a strong oxidant, and hydroquinone, a strong reductant. That is why the former increased the vulnerability of the plants, while the latter decreased it in timothy grass. The positive effect of potassium ferricyanide on plant resistance may be attributed to its role as an inhibitor of oxidation processes of sulfhydryl groups of many enzymes and proteins.

Conclusions

1. Under the influence of acid gases and poisoned soils, the development of fescue and timothy growing near a chemical plant is retarded.

2. Fertilizers can be used to regulate the growth and development of plants and their gas resistance.

3. The role of individual nutrient elements (N, P, K and their combinations) depends on the biological characteristics of the species, as well as on gas resistance, on the stages of growth and development, on the nature of soils, and on the weather and climatic conditions of the season. A positive influence of nitrogen on the gas resistance of forage plants was observed in connection with its important role in protein metabolism.

4. The gas resistance of plants can be increased by means of physiologically active compounds and fertilizers applied by the foliage nutrition method. Potassium ferricyanide, hydroquinone, NaOH, and malic and citric acids were found to have a positive influence.

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EFFECT OF MINERAL NUTRITION ON CERTAIN PHYSIOLOGICAL-BIOCHEMICAL CHARACTERISTICS AND GAS RESISTANCE OF FORAGE GRASSES

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Alongside with the selection of an assortment of resistant plants, the development of methods of increasing the gas resistance of plants assumes a great importance since many industrial enterprises have grounds where not only woody but also forage plants are unable to grow. Acid gases and toxic dust are accumulated by the soil, decreasing its fertility (Wentzel, 1959) and curtailing the activity of the useful microflora (Kulagin, 1964). V. Kroker (1950) noted that the roots of plants sometimes suffer more seriously from industrial pollutants than do the leaves. Inhibition of the growth of root hairs can be observed on poisoned soils (Ryabinin, 1965). All this impairs the mineral nutrition of plants and leads to the accumulation of certain toxic elements - Zn, Pb, Cu (Nemec, 1958) and to a decrease in the viability and resistance of plants to extreme factors (Kulagin, 1968).

In order to improve the conditions of growth and development of plants, practical gardeners change the topsoil regularly, i.e., once every 2 to 3 years, at the copper-smelting plants of the Middle Urals (Krasnoural'sk, Kirovograd, Revda). We established earlier (Nikolayevskiy, 1964) that within 2-3 years fertile soils imported to the copper-smelting plants become quite similar in their agrochemical properties to those of the local poisoned soils.

In the Soviet Union and abroad (Guseva, 1950; Mashinskiy, 1953; Nemec, 1957; Freebairn and Taylor, 1960; Kazantseva, 1965; Ryabinin, 1965; Kisser, 1968) studies were conducted on various methods of increasing the gas resistance of plants. Soil neutralization (liming), application of fertilizers to the soil (K, P, N, Ca), leaf nutrition, and the action of various compounds such as OP-7, sucrose, urea, and potassium ascorbate were found to have a positive effect. The literature contains data to the effect that plants are capable of adapting to the action of acid gases (Levitskaya, 1955; Bulgakov, 1958). On the other hand, methods of growing the plants (Mashinskiy, 1953) and the experience of practical gardeners indicate that the gas resistance of plants can be increased by means of advanced agricultural field practices.

The role of individual elements of mineral nutrition (N, P, and K) in plant life varies. The biochemical role of nitrogen in plants is related to the important part that it plays in protein and nucleic metabolism, which determines the plants' physiological-biochemical and genetic characteristics. The anion of phosphoric acid enters into the composition of many important organic compounds (phospholipids and phosphatides, ATP and ADP, etc.). It participates in many energetic processes that take place in the cells. Potassium in plants regulates the ionic and water regime of the cell and the permeability of the cell membranes. Both the individual elements of mineral nutrition and their definite combination are important for the plants as a function of their growth and development. The deficiency of certain elements in the soil causes an impairment of metabolism and of the form-development processes, and this may be reflected in the gas resistance of plants.

Our studies (Yatsenko, Nikolayevskiy, Firger, and Suslova, 1968), both under experimental conditions in the university botanical garden and under field conditions (at industrial plants) showed that nitrogen fertilizers increase the gas resistance of plants, whereas phosphorus and complete fertilizers (NPK) decrease it. Of great interest is the study of the nature of the influence of fertilizers on the physiological-biochemical characteristics of plants for the purpose of determining the mechanism of their effect on gas resistance. With the exception of an article by Guseva (1950), the literature offers no data on this problem. However, Guseva does not give the results for all types of fertilizers, but only for two forms of nitrogen fertilizers ($NaNO_3$ and $NH_4)_2SO_4$).

In 1967, in the botanical garden, we employed a field method in a study of the influence of mineral nutrition on certain physiological-biochemical characteristics and gas resistance of forage grasses.

Method of Investigation

Two species of forage grasses differing in gas resistance were preselected for the studies: the meadow fescue (Festuca pratensis Huds) as the resistant species and timothy (Phleum pratense L.) as the nonresistant species. The seed was sown on poor sandy soils on May 7, 1967 in accordance with an 8-treatment scheme: control, N, P, K, NP, NK, PK, and NPK in three replications. The size of the plots was 2 m x 2 m. Before the seeding, fertilizers were applied in the proportion of N 4 g, P 6 g, and K 9 g per m^2. Starting on July 10, the plants were watered once a week with solutions of fertilizers in the same proportions; this was followed by a study in relation to (a) their vulnerability in a gas chamber, (b) the quantity of oxidizable substances in the leaves, according to the method of N. P. Krasinskiy (1950), (c) the content of ascorbic acid, after Sapozhkova (1966), (d) the total acidity, after Yermakov and Arasimovich (1952), the oxidation-reduction potential on LPU-0.01, and (e) the water-holding capacity, after Nichiporovich (1926).

Effect of Mineral Nutrition on the Vulnerability

Treatments	Phases, Dates, and											
	Tillering				Booting				Heading			
	23/VI SO_2 — 1/250	24/VI SO_2 — 1/250	27/VI SO_2 — 1/250	Average Plant Vulnerability	7/VII SO_2 — 1/500	10/VII SO_2 — 1/500	11/VII SO_2 — 1/1000	Average Plant Vulnerability	13/VII SO_2 — 1/1000	17/VII SO_2 — 1/1000	19/VII SO_2 — 1/1000	Average Plant Vulnerability
												Timothy
Control	20,0	75,7	85,3	60,3	64,9	92,0	71,3	76,1	58,8	77,8	87,9	74,8
N	23,0	82,0	89,0	64,7	57,6	97,0	69,5	74,7	80,7	73,3	89,2	81,1
P	43,4	81,4	85,3	70,0	78,2	95,0	78,0	83,7	54,4	77,9	96,3	76,2
K	25,0	81,8	81,5	62,8	60,4	90,5	46,7	65,9	76,2	68,[illegible]	70,3	71,7
NP	18,0	88,5	88,8	65,1	57,2	97,5	76,4	77,0	61,7	66,0	92,4	73,4
NK	45,5	87,2	89,2	74,0	60,7	96,0	72,7	76,5	87,6	67,2	91,0	81,9
PK	34,0	91,8	90,6	72,1	67,2	97,0	70,2	78,1	90,9	94,1	88,0	91,0
NPK	59,0	95,2	84,3	79,5	67,1	93,7	64,3	75,0	91,4	90,9	90,1	90,8
												Meadow Fes-
Control	13,2	74,0	82,0	56,4	60,1	48,6	22,9	43,9	76,7	54,1	63,4	64,7
N	12,0	67,5	87,8	55,8	69,4	75,4	58,0	67,6	78,9	45,1	55,3	59,8
P	15,0	73,7	86,0	58,2	47,2	79,8	48,2	58,4	68,7	55,4	64,4	62,8
K	39,0	69,2	84,2	64,1	53,4	75,3	43,7	57,4	69,4	35,2	64,3	56,3
NP	5,0	79,0	79,2	54,4	62,1	80,5	53,4	65,3	63,6	59,4	44,3	55,8
NK	17,0	67,5	81,2	55,2	55,0	80,5	40,7	58,7	55,6	61,2	59,8	58,9
PK	33,0	81,0	91,7	68,6	64,9	77,5	47,9	63,4	71,2	56,2	75,7	67,7
NPK	29,0	77,5	88,0	64,8	57,5	71,8	45,5	59,3	50,9	66,0	74,9	63,9

Table 1

of Forage Grasses to Sulfur Dioxide

SO_2 Concentrations													
Blooming					Ripening					Aftermath			
24/VII SO_2 — 1/1000	25/VII SO_2 — 1/2000	26/VII SO_2 — 1/3000	27/VII SO_2 — 1/3000	Average Plant Vulnerability	9/VIII SO_2 — 1/3000	12/VIII SO_2 — 1/2000	14/VIH SO_2 — 1/2000	16/VIII SO_2 — 1/2000	Average Plant Vulnerability	21/VIII SO_2 — 1/3000	23/VIII SO_2 — 1/3000	25/VIII SO_2 — 1/3000	Average Plant Vulnerability
Grass													
97,2	32,4	49,4	41,4	55,0	17,9	25,2	35,4	57,2	33,9	10,9	18,3	18,1	15,8
96,7	72,3	45,2	74,2	72,1	18,0	39,4	17,3	77,3	38,0	16,3	36,1	50,0	34,1
95,9	32,1	82,3	55,3	66,4	10,3	78,6	24,7	35,4	37,2	—	—	—	—
51,2	27,0	85,0	50,5	53,4	7,9	51,0	19,4	27,2	26,4	47,2	43,2	26,0	38,8
73,2	70,8	47,8	11,2	50,8	3,1	48,4	17,0	38,7	26,8	35,3	40,1	28,6	34,7
84,6	31,1	97,3	33,6	61,6	4,4	41,5	33,3	59,0	34,6	—	—	—	
82,7	19,4	80,0	36,5	54,6	21,0	74,4	55,0	58,0	52,1	8,9	17,1	17,3	14,4
79,5	33,9	94,3	11,8	54,9	37,2	91,3	57,7	76,4	65,6	40,0	21,6	18,1	26,6
cue - tillering													
67,3	41,5	15,6	65,3	47,4	5,2	53,8	71,4	39,9	42,6	30,8	34,5	11,5	25,6
73,0	36,4	19,5	70,5	49,8	4,8	39,4	71,2	57,2	43,2	24,8	43,0	50,1	39,3
71,9	48,6	22,0	56,9	49,8	3,2	10,7	22,9	54,4	22,8	—	—	—	
71,4	55,2	55,5	18,6	50,2	7,4	45,2	19,8	77,1	37,4	46,2	49,8	16,1	37,4
57,2	43,6	30,8	52,4	46,0	3,7	9,2	74,7	52,3	35,0	41,3	25,3	45,2	37,3
51,6	42,7	31,8	18,2	36,1	11,8	12,4	47,8	3,0	18,8	—	—	—	
57,6	33,6	48,4	48,6	47,0	15,1	26,8	64,1	41,9	37,7	36,6	24,2	12,1	24,4
63,1	51,9	48,8	30,5	48,6	18,6	49,2	17,6	74,7	40,0	35,0	11,2	17,1	21,1

We selected these indicators because earlier studies (Krasinskiy, 1950; Guseva, 1950; Nikolayevskiy, 1967) established a correlation between these indicators of plants and their gas resistance. The SO_2 concentration in the polyethylene gas chamber was preselected so as to bring out the differences in the vulnerability of the two types of forage grasses. Sulfur dioxide was obtained through the interaction of a weighed amount of NA_2SO_3 with excess 50% H_2SO_4. The amount of Na_2SO_3 was calculated from the equation $Na_2SO_3 + H_2SO_4 = Na_2SO_4 + SO_2 + H_2O$. To obtain an initial SO_2 concentration of 1/4000 by volume, 0.118 g of Na_2SO_3 was taken; for 1/2000, 0.236 g; for 1/1000, 0.472 g; for 1/500, 0.964 g of Na_2SO_3.

The vulnerability was determined as the ratio of the damaged length of the leaf to the total length in percent. In each treatment of each of the two species, the vulnerability was determined in ten plants in the first three leaves from the top of the shoot. The results were treated statistically by Leont'yev's method (1961).

Results of the Investigation

The species of forage grasses whose gas resistance we studied differ in the biology of growth and development. The meadow fescue is a perennial winter grass, whereas the timothy grass is a "dvuruchki"* (Fedorov, 1968). For this reason, in the first year of life in the case of the meadow fescue, the tests were conducted only during its tillering stage, while in the case of the timothy grass tests were conducted also during the stages of booting (shooting), heading, blooming, and ripening, and in both species after the hay has been cut, i.e., during the period of young aftermath.

In order to bring out more clearly the role of mineral nutrition in the gas resistance of the plants, the latter were sown on poor sandy soils (Table 2).

As is evident from Table 2, the soils of the test area are relatively acid and characterized by an insufficient content of nitrogen and potassium, but are comparatively well-supplied with phosphorus.

The weather-climate conditions of the summer of 1967 (Fig. 1) were favorable for the growth and development of forage grasses, with the exception of August, when an increased solar radiation and irregular precipitation were observed. It is known from literature data (Ivanov, 1936; Kroker, 1950; Krasinskiy, 1950) that an increased solar radiation promotes a greater vulnerability of plants to sulfur dioxide. That is why a change in the vulnerability of the plants (Table 1) was observed in the meadow fescue even during a single stage of growth and development (tillering). The decrease in the gas resistance of the meadow fescue during its first year of life may also be attributed to an increase in the calendar age of the leaves.

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* [Editor's note: Fedorov (1968) states that on the basis of the pattern of their growth-development perennial grasses can be divided into two groups, namely:
(a) winter grasses --- defined as those grasses which do not bear fruit during the year they are sown, and which do not produce a second bloom after hay cutting;
(b) the so-called "dvuruchki" --- defined as those grasses which can bear fruit during the year they are sown, and which can produce a second bloom after the hay has been cut in early summer. The growth-development pattern of these grasses resembles that of the grain crops.]

Table 2

Agrochemical Characteristics of Soils of the Test Area

No. of Soil Cross Section	Depth of Sampling	pH	Hydrolytic Acidity, mg/equivalent	Total Base Absorbed, mg/equivalent	Base Saturation of Soils, %	P_2O_5 After Kursanov, mg/g 100 g	K_2O After Maslova, mg/g 100 g	Nitrogen, %	Humus, %
I	0-20	5.7	3.76	12.5	94.0	51.5	20.0	1.3	6.59
	21-30	5.7	2.88	5.3	65.0	20.0	12.5	0.7	4.96
II	0-20	5.3	4.55	7.5	62.0	50.0	11.6	1.68	8.37
	21-30	4.9	3.76	0.6	13.8	20.0	11.6	0.25	1.73
Optimum values for forage grasses.			0.1-10	10-15	-	50-70	60-90	1.5-2	-

It is evident from Table 1 that a positive effect on the gas resistance of the meadow fescue at the tillering stage was produced at the end of June by N and NP; at the beginning of July, all the fertilizer treatments gave a negative effect, and in the middle of July, N, K, NP, and NK had a positive effect; at the end of July, NP and NK had a positive effect, and on 27 July all the treatments had a positive influence on the gas resistance of the meadow fescue except N. At the beginning of August, a positive effect was obtained in all the treatments except N, and on 12 and 14 August, in all the treatments. At the end of August, all the fertilizer treatments had a negative effect on the aftermath. Hence, a succession of fertilizer treatments having a positive effect on the gas resistance of the plants is observed in the course of 1 year of vegetation in the meadow fescue at the tillering stage. This is quite normal, since the role of the individual elements of mineral nutrition changes during ontogeny as a reusit of growth and development, and also under the influence of weather-climatic conditions and of the water regime of the soils. Thus, the coincidence of the overall positive influence of all the different treatments on the gas resistance of the plants on 27 July and 12-14 August is largely attributable to the character of the weather. On those days, there was a rainy weather, a lower temperature, a decreased solar radiation, and an increased air humidity (Fig. 1). Such a combination of weather conditions is apparently most favorable to the plant's tolerance to the noxious action of acid gases. The positive effect of fertilizers on plant growth (height of shoots, length of leaves) also changes

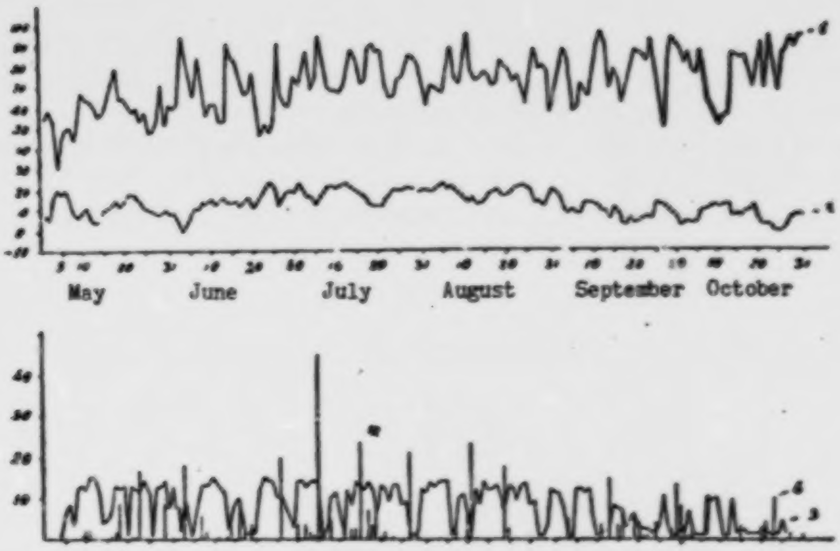

Fig. 1. Meteorological conditions of the vegetation period of 1967 in Perm'.

Notation: 1 - relative humidity of air, %; 2 - mean daily air temperature, °C; 3 - duration of solar radiance, hours; 4 - precipitation, mm.

during the tillering stage in the meadow fescue. At the beginning of summer, an increase in the size of the plants was brought about by P, NK, PK, and NPK, and an increase in leaf size was noted in all the treatments. In the middle of summer, the fertilizers caused a retardation of stem growth and a more vigorous leaf growth. At the beginning of August, the fertilizers caused a decrease in the rate of leaf growth, and in the middle of August, the positive effect of fertilizers on the growth of shoots (N, K, NK) and leaves (N, NP, NPK) reappeared.

The gas resistance of the meadow fescue during its first year of life (tillering) was greatly influenced by nitrogen. The positive role of nitrogen in gas resistance and also in the growth and development of the plants is explained by its major importance in the protein and nucleic metabolism of the plants.

In the course of the annual cycle, the resistance of the timothy (Table 1) first increases toward the booting stage, then decreases (heading, blooming) and again increases for a short time during ripening. Hence, the gas resistance of the plants is not a constant indicator, and varies with the growth and development.

If one compares the action of fertilizers on the gas resistance of the timothy according to the stages of growth and development, one finds that nitrogen increases the gas resistance during the first 2-3 days after the application of fertilizers at all the stages except heading, and that a decrease in resistance occurs on the 4th-5th day. Phosphorus caused a decrease in the resistance of the timothy at all the stages except booting (2nd day) and ripening.

The influence of potassium on the timothy was similar in character to that of nitrogen. Among mixed fertilizers, a positive effect on the gas resistance of the timothy was displayed by NP and NK (blooming and ripening), and PK (heading). The positive influence of fertilizers on the stem growth of the timothy is observed at the beginning of tillering, and on the leaf growth, at the stages of tillering, heading, and blooming. Various fertilizers had a positive influence on the gas resistance of the fescue and timothy, but in both species we noted the positive role of potassium, and in the fescue, that of nitrogen as well. These fertilizers cause a similar increase in stem and leaf growth in both species.

Table 3 shows the dependence of the vulnerability of the plant leaves on the age, i.e., leaf position in reference to height of plant, under the influence of fertilizers.

In the control treatment, the timothy shows a distinct basipetal direction in the vulnerability of the leaves; the fescue shows it less distinctly. Under the influence of fertilizers applied on 29 July 1967 by spraying*, the timothy retained the differences in leaf vulnerability according to leaf position in reference to height, whereas in the meadow fescue, the leaf vulnerability increased in the acropetal direction (with the exception of potassium). This was also observed when the fertilizers were introduced into the soil, but in this case the exception in the meadow fescue was NPK.

Statistical treatment of the differences in the vulnerability of the plants under the influence of the fertilizers showed that in the timothy, close-to-significant differences were produced by N, K, NK and PK, and in the meadow fescue, by N, NP, NK, and PK.

The change in the amount of oxidizable substances in the leaves of forage grasses during ontogeny and the changes taking place under the influence of the fertilizers are presented in Table 4.

It is evident from Table 4 that during the summer, the content of oxidizable substances increases with age in the meadow fescue (tillering stage) and in the timothy, when the latter enters the reproductive stage (heading, blooming), whereas these substances decrease during the ripening stage. In the fescue, even during the tillering stage, the amount of oxidizable substances increases, and in the second half of August, decreases again. The aftermath of both species was found to be more resistant than

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* [Editor's note: foliar nutrition.]

Table 3

Vulnerability of Leaves of Different Ages Acted Upon by Fertilizers and SO_2

Date	No. of Leaf From Top	Treatments							
		Control	N	P	K	NP	NK	PK	NPK
		Timothy							
29/VII	1	33,8	38,2	35,8	44,7	33,3	20,7	32,8	43,2
	2	25,7	41,0	55,3	30,8	30,4	25,1	47,5	52,6
	3	41,7	40,7	28,7	51,0	45,1	47,7	54,1	58,2
	4	75,3	53,3	--	89,0	61,4	—	82,8	64,3
1/VIII	1	30,4	28,9	—	22,3	35,4	—	28,6	28,3
	2	45,6	38,6	—	31,6	89,0	—	45,4	34,7
		Meadow fescue							
29/VII	1	8,4	25,8	32,5	5,5	20,7	43,0	14,7	18,5
	2	13,6	13,1	8,6	12,0	12,2	21,4	15,2	16,9
	3	11,5	14,7	—	14,0	—	—	—	—
1/VIII	1	58,5	28,4	—	20,8	17,7	—	8,9	33,2
	2	56,6	40,7	—	13,9	16,1	—	3,0	55,5

the adult plants. In the timothy, the amount of oxidizable substances and the vulnerability are greater than in the fescue.

A positive effect, i.e., a decrease in the content of oxidizable substances in the timothy was observed under the influence of K. The same treatment also produced a higher gas resistance in the timothy. In the meadow fescue, a similar effect was produced by K, whereas N, PK and NPK caused an increased vulnerability and raised the content of oxidizable substances. The change in the latter under the influence of fertilizers does not always correspond clearly to the change in vulnerability.

In ascorbic acid content, the timothy differs markedly from the fescue (Table 5). As in the case of woody plants, the nonresistant species - timothy - is characterized by a higher ascorbic acid content than the fescue. In both species, the ontogeny shows a direct relationship between the ascorbic acid content and the vulnerability of the plants to sulfur dioxide. However, as in the case of the content of oxidizable substances, the change in the ascorbic acid content under the influence of fertilizers is not always clearly related to the change in the vulnerability of the plants. In the timothy, a decrease in the amount of ascorbic acid and vulnerability is detected only under the influence of NP.

Table 4

Effect of Mineral Nutrition on Differentiated Oxidizability.

Stages and Periods	Control			N			K			NP			PK			NPK		
	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability	Water-Soluble Substances	Water-Insoluble Substances	Vulnerability
Timothy																		
Tillering 7—10/VII	3,6	1,3	78,4	3,8	1,1	77,3	3,8	0,8	75,4	5,0	1,4	77,2	4,1	1,6	81,2	4,4	1,4	80,4
Booting 12—14/VII	4,3	2,5	71,3	3,9	1,0	69,5	3,4	1,1	46,3	4,6	1,2	76,1	3,5	1,8	70,2	4,1	1,1	84,3
Heading 18—25/VII	7,2	3,4	55,1	6,1	2,6	72,8	5,6	2,8	47,8	3,8	3,0	68,4	6,1	3,2	56,8	5,4	2,8	62,4
Blooming 28/VII—9/VIII	3,8	3,3	55,0	2,4	2,8	50,2	2,8	2,2	11,8	2,8	2,4	6,3	3,6	2,4	26,4	4,8	3,2	13,2
Ripening 10—17/VIII	3,8	2,6	33,9	3,3	3,0	38,0	3,9	2,5	42,2	3,8	2,4	33,8	4,1	2,0	50,8	4,3	2,5	65,5
Aftermath 22—31/VIII	4,6	2,2	19,3	3,6	2,1	22,1	2,9	2,6	32,6	2,9	1,8	28,8	3,2	2,6	14,3	2,3	2,4	27,9
Meadow fescue																		
Tillering 7—10/VII	3,0	0,9	54,4	3,3	0,7	72,4	3,5	0,9	64,4	4,4	0,9	71,3	4,1	0,6	71,2	3,8	0,5	66,2
12—14/VII	2,7	1,1	49,8	2,9	1,1	68,4	3,6	1,3	56,6	3,1	1,0	58,5	3,0	0,9	59,6	3,1	1,0	48,2
18—25/VII	2,4	1,3	61,0	3,2	1,4	54,0	4,0	1,5	53,3	2,1	1,4	58,3	2,9	1,5	56,9	3,0	1,3	64,6
28/VII—9/VIII	2,9	2,7	11,8	2,7	2,3	15,1	1,9	1,8	6,6	3,0	2,4	6,5	2,2	2,9	16,8	2,8	2,3	18,8
10—17/V	2,0	2,2	55,0	2,5	1,9	55,9	2,5	1,5	47,4	2,1	1,8	45,4	2,4	1,8	45,3	1,9	2,2	47,2
Aftermath 22—31/VIII	2,1	1,8	24,8	2,4	1,9	33,2	2,2	1,9	42,0	2,1	1,9	33,4	2,2	1,8	27,6	2,3	1,9	20,5

Table 5

Effect of Mineral Nutrition on the Ascorbic Acid Content of Leaves.

Stage and Periods	Control		N		K		NP		PK		NPK	
	Ascorbic Acid	Vulnera-bility	Ascorbic Acid	Vulnera-bility	Ascorbic Acid	Vulnera-bility	Ascorbic Acid	Vulnera-bility	Ascorbic Acid	Vulnera-bility	Ascorbic Acid	Vulnera-bility
Timothy												
Tillering 7—10/VII	27,5	64,9	32,0	57,6	24,0	60,4	27,0	57,2	24,0	67,2	30,0	67,1
Booting 12—14/VII	27,9	65,0	19,2	75,1	21,0	61,2	22,4	68,9	21,4	80,6	23,7	77,8
Heading 18—25/VII	30,2	73,8	28,5	82,4	27,5	77,0	30,4	69,9	31,7	76,7	30,1	81,1
Blooming 28/VII—9/VIII	31,4	42,7	24,8	39,4	23,3	24.7	25,3	5,2	23,7	24,7	22,4	21,2
Ripening 10—17/VIII	17,4	38,9	19,7	44,7	15,4	32,5	17,5	34,7	19,2	62,5	21,8	75,1
Aftermath 22—31/VIII	21,3	19,0	21,8	27,7	20,3	33,7	21,2	28,8	21,0	14,9	20,4	26,0
Meadow fescue												
Tillering 7—10/VII	20,5	54,4	17,0	72,4	16,0	64,4	17,8	71,3	16,5	71,2	17,6	66,2
12—14/VII	14,5	49,8	20,0	68,4	13,7	56,6	15,2	58,5	13,5	59,6	13,5	48,2
18—25/VII	14,7	61,8	13,9	57,8	11,2	57,0	12,9	53,6	10,6	63,2	12,3	68,0
28/VII—9/VIII	12,9	29,6	12,0	35,1	10,9	10,6	12,3	21,8	11,3	27,4	10,4	22,7
10—17/V	12,2	55,0	31,9	55,9	13,3	47,4	10,6	45,4	10,2	45,3	11,8	47,2
Aftermath 22—31/VIII	12,3	22,2	13,5	36,6	17,3	36,8	14,2	35,7	14,3	24,5	15,3	19,8

Table 6

Effect of Mineral Nutrition on Total Acidity.

Stage and Periods	Control		N		K		NP		PK		NPK	
	Total Acidity	Vulner-ability	Total Acidity	Vulner-ability	Total Acidity	Vulner-ability	Total Acidity	Vulner-ability	Total Acidity	Vulner-ability	Total Acidity	Vulner-ability
					Timothy							
Tillering 7—10/VII	3,3	92,0	3,0	97,0	3,0	90,5	3,3	97,5	3,6	97,0	2,8	93,7
Booting 12—14/VII	1,0	58,8	1,5	80,7	1,0	76,0	1,0	61,7	1,3	90,7	1,3	91,4
Heading 18—25/VII	4,7	55,1	2,0	74,8	1,2	47,6	1,3	68,4	1,9	56,8	1,3	62,4
Blooming 28/VII—9/VIII	0,8	55,0	0,5	50,2	0,5	33,1	0,4	12,4	0,6	26,4	0,5	13,2
Ripening 10—17/VIII	0,6	39,3	0,8	44,7	0,5	32,5	0,6	34,7	0,5	60,7	0,9	51,7
Aftermath 22—31/VIII	1,1	19,1	2,0	27,7	2,0	33,7	1,8	28,8	1,8	14,9	1,6	26,0
					Meadow fescue							
Tillering 7—10/VII	2.1	48,6	2,8	75,4	3,4	75,3	3,6	80,5	2,8	77,5	2,8	74,8
12—14/VII	1,6	76,7	2,1	78,9	1,8	69,4	1,1	63,6	1,8	71,2	2,1	50,9
18—25/VII	0,6	47,8	0,6	40,8	0,5	41,9	0,5	57,3	0,5	44,9	0,6	59,0
28/VII—9/VIII	0,5	29,6	0,5	35,1	0,4	10,6	0,4	21,8	0,6	27,4	0,4	22,7
10—17/V	0,5	55,0	0,6	55,9	0,5	39,8	0,4	53,7	0,5	45,3	0,6	47,2
Aftermath 22—31/VIII	1,9	22,2	2,3	36,6	2,0	36,8	2,0	35,7	2,1	24,5	2,0	19,8

Table 7

Dynamics of the Oxidation-Reduction Potential and Gas Resistance During the Vegetation Period Under the Influence of Fertilizers.

Stages and Periods	Control				N				K				NPK			
	pH	Eh	rH_2	Vulnera-bility	pH	Eh	rH_2	Vulnera-bility	pH	Eh	rH_2	Vulnera-bility	pH	Eh	rH_2	Vulnera-bility
							Timothy									
Heading 17—24/VII	6,81	0,273	22,91	73,8	7,00	0,285	23,79	82,4	7,05	0,292	24,11	80,1	7,13	0,295	24,32	81,1
Blooming 17/VII—9/VIII	6,87	0,286	23,62	42,7	6,73	0,271	22,73	39,6	6,51	0,263	22,05	24,7	6,62	0,267	22,40	21,2
Ripening 10—17/VIII	5,61	0,214	18,60	46,3	5,76	0,218	19,08	47,3	6,10	0,242	20,55	23,3	6,30	0,255	21,35	67,0
Aftermath 21—30/VIII	6,10	0,244	20,66	19,0	6,16	0,247	20,83	27,7	6,17	0,244	20,71	33,7	6,29	0,256	21,37	26,0
							Meadow fescue									
Tillering 17—24/VII	6,47	0,259	21,84	64,7	6,61	0,263	22,28	59,8	6,80	0,276	23,07	56,3	6,60	0,261	22,18	63,9
27/VII—9/VIII	6,44	0,258	21,74	21,7	6,42	0,257	21,63	22,2	6,54	0,262	22,08	20,6	6,42	0,257	21,63	29,9
10—17/VIII	6,22	0,248	21,00	62,6	6,25	0,250	21,10	55,3	6,18	0,245	20,80	32,5	6,42	0,260	21,74	33,4
Aftermath 21—31/VIII	5,96	0,233	19,93	22,2	6,23	0,250	21,04	36,6	6,00	0,235	20,08	36,8	6,28	0,255	21,30	19,8

Table 8

Effect of Mineral Nutrition on the Water-Holding Capacity of Leaves (Percent of Water Held for 2 Hours).

Control		N		K		NP		PK		NPK	
Water-Holding Capacity, %	Vulnerability	Water-Holding Capacity, %	Vulnerability	Water-Holding Capacity, %	Vulnerability	Water-Holding Capacity, %	Vulnerability	Water-Holding Capacity, %	Vulnerability	Water-Holding Capacity, %	Vulnerability
Timothy											
11 July — Tillering Stage											
39,9	92.0	35,4	97,0	49,8	90,5	42,2	97,5	49,1	97,0	52,0	93,7
13 July —Booting Stage											
62,0	58.8	70,9	80,7	59,6	76,2	61,9	61,7	63,9	90,9	67,4	91,4
Meadow fescue											
11 July — Tillering Stage											
45,3	48,6	46,4	75,4	55,9	79,8	44,2	75,3	48,2	80,5	44,9	80,5
13 July. — Tillering Stage											
58,6	22,9	61,0	58,0	72,9	43,7	57,9	53,4	52,9	47,9	62,0	45,5

In forage grasses, a decrease of the total acidity with age is observed during the ontogeny. The resistant species - meadow fescue - is characterized by a lower total acidity than the timothy. At the same time, the seasonal dynamics of the total acidity and vulnerability are reversed as compared with the differences between the species, i.e., a decrease of total acidity in both species is associated with an increased vulnerability. Fertilizers caused an increase of the total acidity in the meadow fescue and a decrease in the timothy. No distinct relationship was observed between the change of the total acidity and vulnerability under the influence of the fertilizers.

A study of the oxidation-reduction potential showed that in the meadow fescue and timothy, the values of the protoplasm pH, Eh and rH_2 do not reflect any relationship to the gas resistance.

The water-holding capacity, which characterizes the resistance of protoplasmic biocolloids, shows a direct correlation to the gas resistance of plants (Nikolayevskiy, 1967). In the meadow fescue and timothy (Table 8), a direct relationship was observed between the gas resistance of the plants and their water-holding capacity (control, 11 and 13 July). There was a significant difference in water-holding capacity between the species as well. In the meadow fescue, an increase of the water-holding capacity was caused by K, and in the timothy, by K (11 July), PK, and NPK. However, the increase in the water-holding capacity under the influence of the fertilizers is frequently associated with an increase in vulnerability; this is difficult to explain, considering the correlation between the water-holding capacity and vulnerability of plants (Nikolayevskiy, 1967).

Conclusions

1. The studies established the feasibility of regulating the gas resistance of plants by means of mineral nutrition. A positive effect was obtained in forage grasses by the application of nitrogen and potassium. The positive effect of nitrogen is apparently due to its important role in protein metabolism, and that of potassium, to its role in the regulation of the permeability and ionic regime of the protoplasm.

2. During ontogeny, because of a change in the plants' requirements for the various nutritional elements, a regular succession of the types of fertilizers that have a positive effect on the gas resistance is observed.

3. As established by a number of investigators, the indicators of plant gas resistance (oxidizability, ascorbic acid, water-holding capacity, oxidation-reduction potential) can be used to characterize species differences in the gas resistance of forage grasses.

Under the influence of fertilizers, the change of these indicators does not always exactly coincide with the change in the gas resistance. This makes it necessary to postulate that they are connected only indirectly with the mechanism of plant resistance.

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EXPERIENCE IN THE USE OF THE BIOCHEMOLUMINESCENCE METHOD FOR DIAGNOSING THE GAS RESISTANCE OF PLANTS

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The hypotheses of K. Hoaka and N. P. Krasinskiy (1950) explain the formation of gas burns on leaves by oxidation processes in chlorophyll-bearing plant tissues. Krasinskiy's proposed method of determining the amount of oxidizable substances in plants in an acid medium, which he identified with the activity of oxidation processes in plants under the influence of sulfur dioxide and light, is not very reliable. This method is biochemically primitive. While it enables one to judge the nature of the oxidation processes in plant cells under the influence of sulfur dioxide it does not permit an identification of the biochemical composition of the substances undergoing oxidation or the ascertaining of the sequence and degree of their oxidation.

The appearance and development of the new biochemoluminescence method in biophysics (Tartusov, Ivanov, and Petrusevich, 1967) opens up new opportunities for the study and interpretation of the biochemical aspect of oxidation processes in plants under the influence of sulfur dioxide. A set of electronic instruments with a high sensitivity FEU-42 photomultiplier are used to record spontaneous and induced oxidation processes in plants. The extremely faint luminescence detected by the photomultiplier is amplified with an USh-2 amplifier and recorded with a pulse counter.

According to present day understanding (Tarusov et al., 1967), the ultrafaint luminescence of plants is due to spontaneous oxidation processes in the cell biolipids. Many oxidation processes in cells have been found to be associated with luminescence. Despite the fact that only a small number of the molecules that participate in the reaction, luminesce, the luminescence reflects the kinetics of the given reaction. Consequently, the measurement of chemoluminescence will permit the determination of kinetic parameters and the interpretation of the mechanism of oxidation processes. It was found (Agaverdiyev, Tarusov, 1965) that the luminescent activity of plants reacts sharply to the slightest shifts in ecological conditions (temperature, composition of air, humidity, etc.).

Since the ultrafaint luminescence is recorded by the photomultiplier only in etiolated plants, we attempted to study the differences in the ultrafaint luminescence of plants and certain biochemical characteristics (12 species of forage plants) and also the change of ultrafaint luminescence under the steady influence of different concentrations of sulfur dioxide. In the latter case, use was made of 4-10-day etiolated sprouts of meadow fescue and timothy grass, which differ markedly in gas resistance in the green state. The first species is resistant to SO_2, and the second is nonresistant. We studied the vulnerability of green (SO_2 concentration 1/400 by volume) and etiolated (concentration 1/500) plants aged 8 days, as well as the amount of substances oxidizable by 0.1 N $KMnO_4$ by Krasinskiy's method (1950), the intensity of ultrafaint luminescence based on green and dry weight and on a single plant, and the water content of the plants. The ultrafaint luminescence was determined in the course of 10 sec in four replications. In the study of the influence of various SO_2 concentrations (0.001%, 0.01%, 0.1%, 1%, 10%, 100%) on the luminescence of plants, we recorded first the luminescence before the action SO_2 (control), and then from the start of the action of the gas for 10 minutes at 30 sec intervals. The plants were grown in Petri dishes on filter paper.

The studies showed that the plants in the etiolated and green states have different gas resistances. It was found that in order to observe clear-cut differences in vulnerability to the gas, the etiolated sprouts require an SO_2 concentration 8-10 times greater than the green sprouts. On the other hand the high resistance to SO_2 in plants in the green state also is not always retained in etiolated plants (Table 1).

According to Krasinskiy (1950), there is no distinct relationship between the gas resistance of green and etiolated sprouts and the content of oxidizable substances.

An inverse relationship was observed between the gas resistance of etiolated sprouts of the cereals and their ultrafaint luminescence, based on 1 g of green and dry substance, and a direct relationship to the luminescence was found based on one plant (Table 1). Hence, the stronger the free oxidation in tissues, the lower the resistance of the plants to sulfur dioxide. A direct dependence between the luminescence and gas resistance in the calculation based on one plant can apparently be explained by differences in the size and mass of a single plant in different species (the gas-resistant plants had larger sprouts). Under the influence of SO_2, the ultrafaint luminescence of plants changes as a function of the gas concentration, and hence, as a function of the amount of sulfur dioxide absorbed by the sprouts. Even a minimum SO_2 concentration (0.001%) activates the luminescence. As the SO_2 concentration rises (to 10%), the activation of ultrafaint luminescence in the plants increases. Concentrated sulfur dioxide (100%) causes a depression of the luminescence of sprouts. A depression of the luminescence of sprouts with 100% SO_2, as well as its activation at lower gas concentrations (10%, 1%, 0.1%), show a certain relationship to the vulnerability of the plants. In the resistant species, meadow fescue, there is a smoother depression of luminescence with 100% SO_2, and a greater activation by the gas in concentrations of 10%, 1%, and 0.1%. In the less resistant species, timothy grass, a sharper depression of luminescence with 100% SO_2 and a relatively weaker activation of luminescence with 10%, 1%, and 0.1% SO_2 were observed.

Table 1

Some Characteristics of 8-day Sprouts of Forage Grasses and Their Gas Resistance.

Species	Vulnerability of Green Sprouts in % of Leaf Length	Vulnerability of Etiolated Sprouts in % of Leaf Length	Amount of Oxidizable Substances in 1 g of Green Weight of Etiolated Sprouts		Intensity of Ultrafaint Luminescence, Pulses per 10 sec, Based on:		
			Water-Soluble Substances	Water-Insoluble Substances	1 g of Green Weight	1 g of Dry Weight	1 Plant
Meadow fescue	2	8,8	0,65	0,I5	296	3020	I,79
Pasture ryegrass	I5,5	6,5	0,59	0,24	325	2742	I,72
English ryegrass	6	6,3	0,55	0,20	I25	2930	I,67
Common fescue	5	I4,7	-	-	I26	1630	0,82
Awnless brome grass	23	-	-	-	274	3023	2,5
Red-top fiorin	-	100	0,64	0,I8	625	31245	2,14
Orchard grass	9,8	I4,4	0,7	0,I8	5I6	46I8	2,22
Meadow foxtail	26	9,3	0,3	0,I2	318	4756	0,9
Timothy grass	38	I5,1	I,I	0,I5	306	2839	0,62
Creeping quackgrass	20	7,9	0,3	0,I8	304	3666	3,II

The above studies showed that the biochemoluminescence method can be used to record the effect of toxic gases (SO_2) in concentrations below 1 ppm (0.0001%) on etiolated plants. Hence, this method of diagnosing the toxic effect of gases on plants is more than 10 times as sensitive as the method of influence on photosynthesis, proposed by Thomas and Hill (1937).

Conclusions

1. It was found that etiolated plants of forage grasses are more resistant to SO_2 than green plants. Damage to etiolated plants by sulfur dioxide requires concentrations 10 times as high as those required for green plants.

2. In etiolated plants there is no relationship between the amount of substances oxidized by 0.1 N $KMnO_4$ in 1 gram after Krasinskiy (1950) and the vulnerability of plants to sulfur dioxide.

3. Under the influence of SO_2 (conc. from 0.001% to 10%), the luminescence in etiolated plants increases. The activity of the luminescence is more pronounced in the resistant species - fescue, and less pronounced in timothy grass. Concentrated sulfur dioxide depresses the luminescence of both species.

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GAS RESISTANCE AND CERTAIN BIOCHEMICAL CHARACTERISTICS OF ETIOLATED AND GREEN PLANTS OF FORAGE GRASSES

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The mechanism of oxidation processes in plants under the influence of SO_2 has not been studied thoroughly thus far. Despite the considerable time that has elapsed since the publication of the works of K. Noack (1920), who assumed that sulfur dioxide causes the development of photodynamic oxidation processes in light, the character of these processes is unclear nor are we too clear as to the biochemical composition of the "oxidizable" substances determining the gas resistance of plants after N. P. Krasinskiy (1950). For this reason, neither Krasinskiy's term "oxidizability" nor his method of determination have attained a serious consideration among physiologists and biochemists.

At the present time it has been established that SO_2 depresses the photosynthesis of plants (Ivanov, 1936; Thomas and Hill, 1937), increases the respiration and the respiratory quotient (Zheleznova-Kaminskaya, 1953; Ryabinin, 1962), inhibits the action of the enzymes enolase, phosphatase, amylase, and catalase (Fortunatov, 1968; Nikolayevskiy, 1968; Nikolayevskiy and Suslova, 1968), and enhances the activity of terminal oxidases, peroxidase and polyphenol oxidase; the oxidation of sulfide is accomplished at the expense of carbohydrates, according to Hazelhorf and Lindau (cited by Krasinskiy, 1950). Under the influence of SO_2, an enhancement of the reducing properties and of the pentose phosphate oxidation route in respiration has been observed in resistant plants. In nonresistant plants, an enhancement of the oxidizing properties and of the Krebs cycle was observed (Nikolayevskiy and Suslova, 1968; Nikolayevskiy, 1968). The advantage of the apotomical method of oxidation in the resistance of plants to extreme factors is explained by the important role of pentoses and hexoses in the utilization of toxic products. Hence, resistant plants are characterized by a greater buffering capacity of the protoplasm and a faster oxidation of SO_2 to the sulfate, so that the toxicity of SO_2 is reduced almost 30-fold (Tomas, 1962). In nonresistant plants, the oxidation of the anion of SO_2 appears to be retarded.

Many indicators of plant gas resistance such as the content of oxidizable substances, ascorbic acid, oxidation-reduction potential, water-holding capacity and others proposed by various authors (Krasinskiy, 1950; Nikolayevskiy, 1964) are only indirect and correlational, and thus do not always reliably characterize the resistance of plants to SO_2.

Great possibilities for the study of the mechanism and chemistry of photodynamic oxidations in plants were opened up by the development of a new biophysical method of recording ultrafaint luminescence. The study of the mechanism of oxidation processes under the influence of SO_2 will make it possible to find direct indicators for an exact evaluation of the resistance of plants. It has been found that the activation of luminescence is the result of the oxidation of a substrate, and a decrease of luminescence signifies a decrease of the oxidative processes or the closeness of the object to death. It is postulated that the source of ultrafaint radiation is the spontaneous oxidation of cell lipids (Zhuravlev, Polivoda, and Tarusov, 1961).

Dark chemiluminescence makes it possible to estimate the general level of physiological activity of cells and tissues (Vladimirov and L'vova, 1965) the change in the state of certain functional systems, the viability of certain tissues (B. N. Tarusov, I. I. Ivanov, and Yu. M. Petrusevich, 1967), the mitotic activity of cells, the frost resistance, heat resistance, and gas resistance of many plants (Gasanov et al., 1963; Agaverdiyev et al., 1965; Agaverdiyev and Tarusov, 1955; Nikolayevskiy and Miroshnikova, 1968), and the antitumor and radiation-protection properties of certain substances (Tarusov et al., 1968). The biochemiluminescence method may be used to ascertain (a) the temperature range of the life of various plant species (Veselovskiy, 1963; Agaverdiyev, Doskach, and Tarusov, 1965), (b) the sublethal and lethal concentrations of toxic gases for plants (Nikolayevskiy and Miroshnikova, 1968), and (c) the various links in the biochemical chain of oxidation processes under the influence of acid gases.

Making use of the new method we attempted to study the mechanism of the action of sulfur dioxide on etiolated and green plants and to determine the possibility of diagnosing the gas resistance of various plants.

Method of Investigation

The studies were conducted on etiolated and green plants of the meadow fescue (Festuca pratensis Huds.) (a resistant species) and timothy (Phleum pratense L.) (a nonresistant species). The plants were grown in Petri dishes on filter paper at t = +20°C. Plants aged 4, 6, 8, 10, and 12 days were used for the experiments. Alongside with the ultrafaint luminescence, investigations were made of the amount of oxidizable substances after N. P. Krasinskiy (1950), the content of ascorbic acid after Sapozhkova (1966), and the vulnerability of the plants to sulfur dioxide (Nikolayevskiy and Suslova, in press). The isotopic method was used for an exact determination of the amount of gas absorbed. The plants were gassed with 0.35% sulfur dioxide having a specific activity of 2 microcuries per liter in the course of 1 hour. Twenty-four hours later, the vulnerability and activity of $S^{35}O_2$ were determined in 10 plants on a B-2 instrument using an SBT-7 end-window counter at a voltage of 380 volts. The determination of the ultrafaint luminescence was carried out on a quantum-measuring device consisting of a highly sensitive photomultiplier FEU-42, USh-2 amplifier, PP-15 radiometer, and VS-22 high-voltage rectifier. Plants weighing 3-5 g were placed in a beaker which was connected via micro-vacuum pumps to a closed system containing SO_2 in concentrations of 100%, 10%, 1%, 0.1%, and 0.001% by volume. The luminescence without the gas was recorded first (control), then the gas was introduced, and the change of luminescence was recorded for 10 minutes (experiment). In the work with green plants, the spontaneous luminescence was measured first (it was usually at the level of the background), then the plants were illuminated with an OR-19 illuminator for 5 sec, and the luminescence was recorded again. After the luminescence fell to the minimum (4 minutes), sulfur dioxide was introduced (100%, 10%, 1%, 0.1%, and 0.01% by volume), the luminescence being measured at the same time. After the luminescence caused by the action of SO_2 decayed, the plants were again illuminated with light from OR-19 (5 seconds), and the new luminescence was recorded.

Results of Investigation

Two species of forage grasses differing sharply in resistance in both the green and the etiolated state were selected by preliminary experiments. Earlier, we established (Nikolayevskiy and Miroshnikova, 1968) a certain inverse relationship between the gas resistance of etiolated eight-day sprouts of cereals and their ultrafaint luminescence per one gram of green and dry matter, and a direct relationship with the luminescence per plant.

It is known from literature data (Krasinskiy, 1950; Nikolayevskiy, 1963, 1965) that the amount of substances oxidizable with a 0.1 N solution of $KMnO_4$ and the ascorbic acid content of plants are indicators of their gas resistance. In resistant plants there are less oxidizable substances and ascorbic acid per gram of green or dry substance. We attempted to study the reliability of these indicators for green and etiolated sprouts of forage grasses in relation to their age and gas resistance (Table 1).

It is evident from Table 1 that the vulnerability of plants of both species in the etiolated and green states increases regularly from the four-day to the eight-day age, then decreases. Both etiolated and green sprouts of the meadow fescue were found to be 2-3 times more resistant than those of the timothy. Etiolated plants of both species were found to be more resistant than green ones. The fact that the retention of species differences in the vulnerability of the plants is pronounced even in the etiolated state indicates that the gas resistance is a constant species indicator.

Table 1

Some Biochemical Characteristics of Sprouts of Forage Grasses and Their Gas Resistance in Relation to Age.

Age, Days	Etiolated Plants					Green Plants				
	Amount of Substances Oxidizable with 0.1 N Solution of $KMnO_4$ per gram of green Substances			Ascorbic Acid, mg %	Vulnerability, %	Amount of Substances Oxidizable with 0.1 N Solution of $KMnO_4$ per Gram of Green Substance			Ascorbic Acid, mg %	Vulnerability, %
	Water-Soluble Fraction	Water Insoluble Fraction	Total Content			Water-Soluble Fraction	Water-Insoluble Fraction	Total Content		
	Meadow Fescue									
4	0,95	0,15	1,1	0,23	2,8	1,25	0,25	1,5	0,64	7,1
6	0,85	0,4	1,25	0,17	3,4	0,9	0,65	1,55	0,37	21,7
8	1,1	0.45	1,55	0,18	7,7	0,9	0,4	1,3	0,23	18,5
10	0,85	0,65	1,5	0,19	5,1	1,45	0,35	1,8	0,27	10
12	0,35	0,2	0,55	0,16	4,2	—	—	—	—	—
	Timothy									
4	0.85	0.1	1,05	0,15	6,8	2,05	0,2	2,25	0,29	19,0
6	0,7	0,8	1.5	0,18	10,6	1,05	0,95	2,00	0,50	26,5
8	0,85	1,3	2,15	0,19	14.6	0,95	0,55	1,50	0,20	24.4
10	0.9	1.65	2,55	0,20	12,1	1,25	0,45	1,7	0,30	14,1
12	0,22	0,3	0,52	0,10	17,0	—	—	—	—	—

On the other hand, this makes it possible to studv the resistance of plants by means of the biochemiluminescence method. The retention of species differences in the gas resistance of plants in the etiolated state makes it necessary to assume the presence of a relationship not only to photosynthesis, but also to some other species characteristics, in particular, to the stability and buffering capacity of the cell content, i.e., proteins and biocolloids of the protoplasm and organoids.

The amount of ascorbic acid in etiolated plants increases with age up to 10 days, and decreases in the 12-day sprouts. In green plants, there is no distinct pattern of change in the content of ascorbic acid with age. In both cases, the meadow fescue contained less ascorbic acid (with the exception of the four-day age) than the timothy, this being in accord with our conclusion (Nikolayevskiy, 1964) that the gas resistance of plants is dependent on the ascorbic acid content. The latter is higher in green plants, which is consistent with their greater vulnerability as compared to etiolated plants.

In the water-insoluble fraction, the amount of substances oxidizable by a 0.1 N $KMnO_4$ also increases with age. In the meadow fescue, their content is less than in the timothy in the etiolated and green states, this being in accord with Krasinskiy's conclusions (1950). However, in the etiolated timothy, the content of oxidizable substances was found to be higher than in the green timothy.

Thus, the indicators of gas resistance of plants proposed by Krasinskiy (1950) and us (Nikolayevskiy, 1964), i.e., the amount of substances oxidizable by a 0.1 N solution of $KMnO_4$ and ascorbic acid can indeed characterize the gas resistance in individual species of plants.

In another experiment (Table 2) we attempted to study the vulnerability and accumulation of sulfur in plants by means of the isotopic method. The plants were gassed with labeled sulfur dioxide ($S^{35}O_2$) of low specific activity.

It is evident from Table 2 that, as in the preceding case, the etiolated plants are more resistant than the green ones, and the meadow fescue is more resistant than the timothy in both cases. The vulnerability of the plants changes with age: the four and ten day old sprouts were injured less, and the six and eight day ones more. It was found that the activity of live and dry plant leaves per gram of dry substance was directly proportional to the vulnerability of the plants. Hence, the nonresistant species accumulate $S^{35}O_2$ up to the lethal level more rapidly, and are therefore more extensively injured by gases.

Table 2

Absorption of $S^{35}O_2$ by Plants of Forage Grasses.

Plant Species	Age of Plants, Days	Etiolated Plants				Green Plants			
		Vulnerability, %	Activity of One Live Plant	Activity of Ten Dry Plants	Activity of 1 g of Dry Weight	Vulnerability, %	Activity of One Live Plant	Activity of Ten Dry Plants	Activity of 1 g of Dry Weight
Timothy	4	6,8	9,0	10,3	20600	19	10,2	208	148570
	6	10,6	8,6	95	35185	26,5	16	100	41666
	8	14,6	21	365	331818	24,4	19	292	194066
	10	12,1	12	172	148333	14,1	14,6	175	116666
	12	17,0	13,6	175	145831	14,1	24	282	176280
Meadow Fescue	4	2,8	24	236	57561	7,1	11,6	346	182600
	6	3 4	18	292	139047	21,7	30,1	107	63000
	8	7,7	27	496	215652	18,5	28,6	435	217500
	10	5,1	17	235	87037	10	30	440	193900
	12	4,2	22	494	176428	4,2	20	387	154800

A new, interesting phenomenon was observed (Table 2). It was found that in the green plants of the timothy, whose vulnerability is on the average greater than that of the meadow fescue, the activity of S^{35} in the leaves was 30% lower per plant, and 19% lower per gram of dry weight. This was also observed in a comparison of the etiolated plants. Even in the case of the same activity, the fescue is injured by sulfur dioxide less than the timothy. Hence, the lethal limit of accumulation of sulfur dioxide in the meadow fescue is higher than in the timothy. This may be attributed to a higher stability of the proteins and biochemical structures in the cell and a higher metabolism in the meadow fescue than in the timothy.

We verified the activity of sulfur in plant roots and ungerminated seeds. It was noted that the amount of labeled sulfur was 2-3 times greater in the roots of green plants than in those of etiolated ones. It may be assumed that green plants can transport the absorbed sulfur in the form of the SO_4 anion into the roots and thence into the soil, thus reducing its content in the leaves. A similar observation was made by Thomas and Hill (1937). In the meadow fescue, the ability to redistribute and eliminate sulfur from the leaves is greater than in the timothy.

Statistical treatment of the data showed that the coefficient of variation v for the activity of S^{35} in the plants was almost always higher than the same indicator for the vulnerability. On the other hand, the coefficient of variation and the accuracy of the experiment (P) for both indicators (vulnerability and activity) vary almost synchronously, i.e., the changes of v and P for the vulnerability indicator coincide with the change of their activity. The accuracy of the experiment fluctuates within the range from 3 to 18%. The differences in vulnerability with age are significant in both species or border on significance, whereas differences in activity are only slightly significant in most cases. The statistical differences in vulnerability between the etiolated and green plants are significant in the fescue and only slightly significant in the timothy. The differences in activity are only slightly significant. Thus, even in the presence of slight differences in the absorption of sulfur dioxide by the plants and in relation to age, significant differences in vulnerability are observed in the majority of cases.

The observation of differences in vulnerability in etiolated plants makes it possible to assume that a change in the ultrafaint luminescence of plants under the influence of SO_2 will characterize their gas resistance. Figures 1-3 illustrate the effect of sulfur dioxide and CO_2 of different concentrations on the ultrafaint luminescence of etiolated plants in relation to their age. From the literature (Agaverdiyev and Bynov, 1968) it is known that 100% CO_2 intensifies the ultrafaint luminescence of cultivated cereals. We were the first to show (Nikolayevskiy and Miroshnikova, 1968) that SO_2 causes an intensification of the luminescence of etiolated plants even at negligible gas concentrations (up to 0.001%).

It is evident from Fig. 1a that in the 8-day etiolated sprouts of forage grasses, a sharp depression of luminescence is observed under the influence of 100% SO_2, and a less marked depression under the influence of 100% CO_2. In the meadow fescue, we even observe at first a slight activation of luminescence under the influence of 100% CO_2. In wheat of the Moskovka variety, as should be expected (Agaverdiyev and Bynov, 1968), a strong activation of luminescence by 100% carbon dioxide and a slight activation by pure sulfur dioxide are observed. Differences in the nature of the action of carbon dioxide and sulfur dioxide may be regarded as the result of the greater chemical activity of SO_2 as compared with that of CO_2 and the greater strength of the acids H_2SO_4 and H_2SO_3 as compared with H_2CO_3, which are formed in the plants upon absorption. This is clearly evident (Figs. 2-3) from the effect of low SO_2 concentrations on the plants. Sulfur dioxide in concentrations of 10% or less caused an activation of luminescence. The detection of a similarity in the effect of the two gases on the ultrafaint luminescence of sprouts provides one more proof of the universal and nonspecific character of the action of gases on plants, manifested in a change of the oxidation-reduction processes under the influence of acidification of the cell protoplasm, and shows that the use of the term "acid gases" is justified (Nikolayevskiy and Kazantseva, 1966; Nikolayevskiy and Yatsenko, 1968).

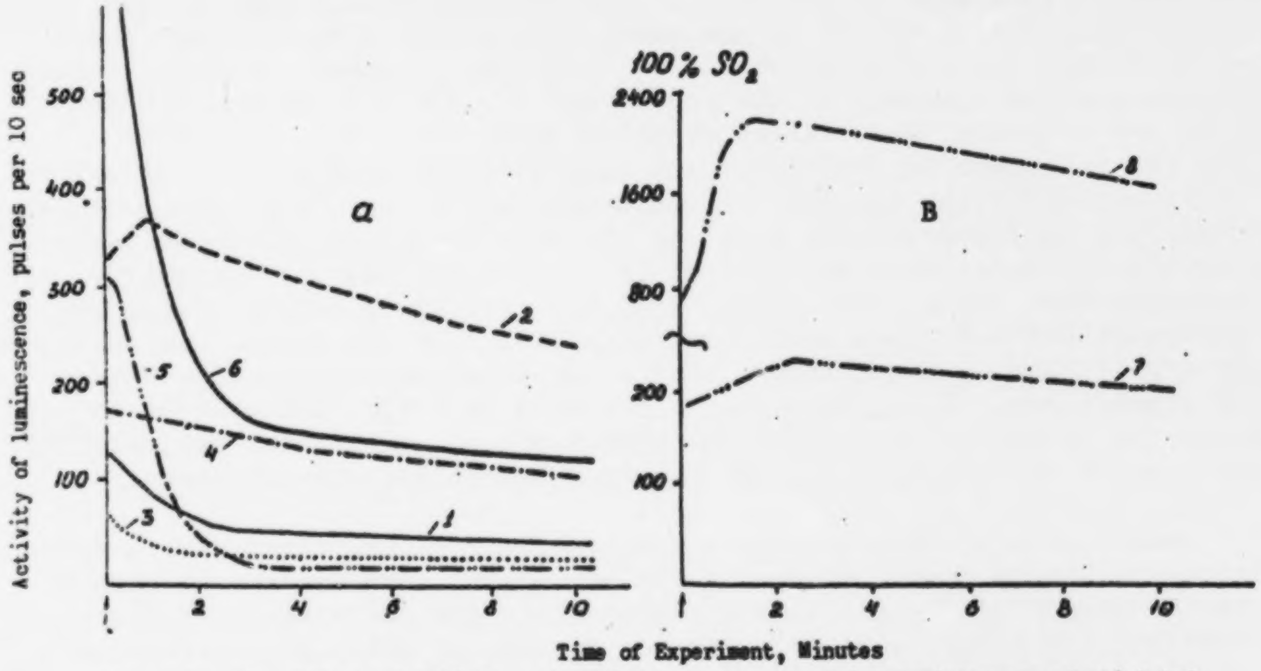

Fig. 1 (a, b). Effect of 100% SO_2 and 100% CO_2 on the ultrafaint luminescence of etiolated sprouts of forage grasses eight days old.

Notation: 1 - meadow fescue - SO_2; 2 - meadow fescue - CO_2; 3 - timothy - SO_2; 4 - timothy - CO_2; 5 - red clover - SO_2; 6 - Red clover - CO_2; 7 - Moskovka wheat - SO_2; 8 - Moskovka wheat - CO_2.

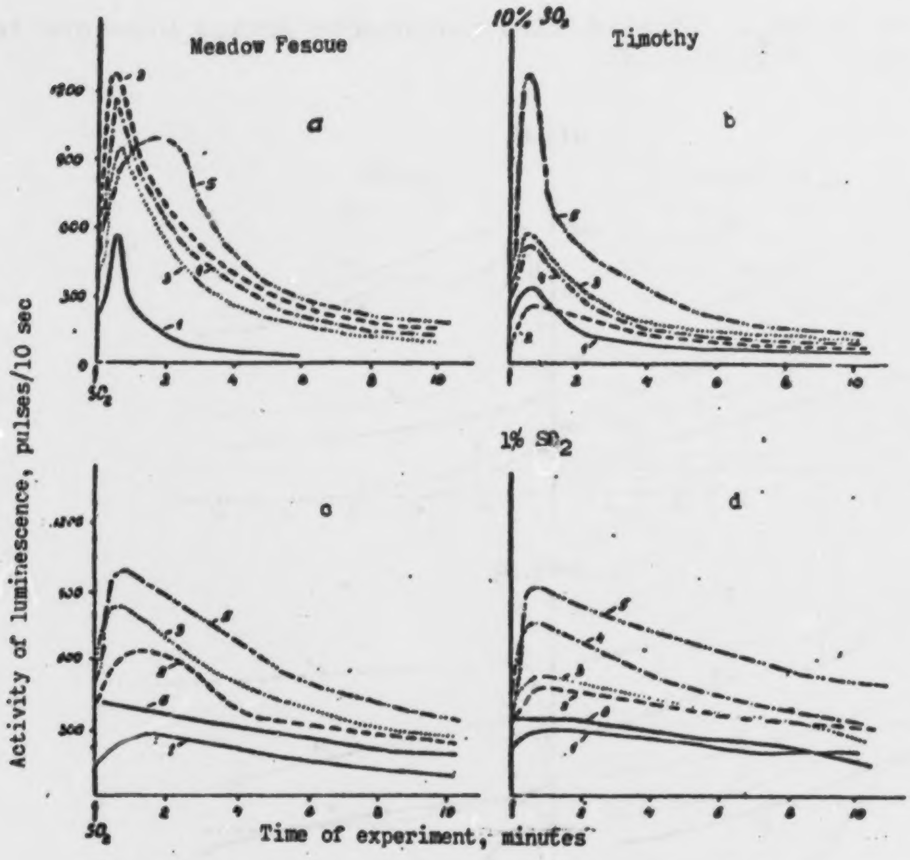

Fig. 2 (a, b, c, d). Effect of different concentrations of SO_2 on the ultrafaint luminescence of etiolated sprouts of forage grasses of different ages.
Notation: a - meadow fescue - 10% SO_2; b - timothy - 10% SO_2; c - meadow fescue - 1% SO_2; d - timothy - 1% SO_2; 1 - age four days; 2 - 6 days; 3 - 8 days; 4 - 10 days; 5 - 12 days; 6 - 8 days (control).

Sulfur dioxide (10%) causes a strong activation of ultrafaint luminescence in etiolated plants of both species, which rapidly changes into depression (Fig. 2 a, b). With age, the activity of luminescence under the influence of 10% SO_2 increases in the plants. The character of the change in the activity of the luminescence of sprouts under the influence of 10% SO_2 with age (Fig. 2 a, b) coincides with the change of their vulnerability to the gas (Table 2). At the same time, the activation of luminescence in the fescue is always greater than in the timothy. This may undoubtedly be attributed to differences in their gas resistance. Their regularity is also observed in the action of other SO_2 concentrations (Fig. 2 c, d, 3 a, b, c, d, e, f).

The experiments have shown that lower sulfur dioxide concentrations also cause an increased luminescence of etiolated sprouts of forage grasses. In these cases, the peak of the luminescence occurs somewhat later after the start of the action of SO_2. This is also noticeable during exposure to 0.001% sulfur dioxide (Fig. 3 e, f).

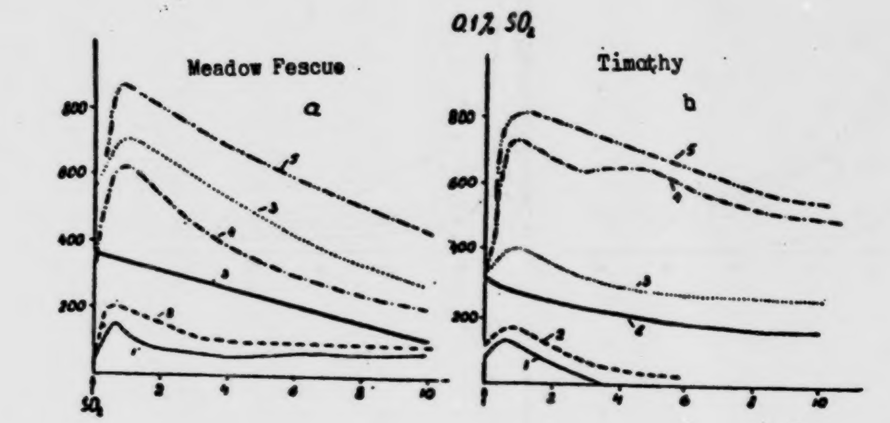

Fig. 3. (a, b, c, d, e, f). Effect of different SO_2 concentrations on the ultrafaint luminescence of sprouts of forage grasses.

Notation: a - meadow fescue - 0.1% SO_2; b - timothy - 0.1% SO_2; c - meadow fescue - 0.01% SO_2; d - timothy - 0.01% SO_2; 1 - age 4 days; 2 - 6 days; 3 - 8 days; 4 - 10 days; 5 - 12 days; 6 - 8 days (control).

A check determination of the luminescence of sprouts of forage grasses in the course of 10 minutes showed that transplanting the plants into beakers and their slight desiccation causes a certain depression of spontaneous luminescence.

Thus, the forage plants, which differ in their resistance to sulfur dioxide, differ also in the activation of luminescence by the gas in the etiolated state. Since in the etiolated state a vigorous vital activity is observed in these plants when they are from 4 to 10-12 days old, (at the expense of the reserved substances stored in the seeds) one observes that the greatest vulnerability of the plants to the gas and the greatest activation of luminescence takes place precisely during the middle of this period (6-8 days).

With the aid of the above-described setup one can diagnose the resistance of plants by using etiolated sprouts. In this case, the degree of resistance can be determined from the relative magnitude of the flash of luminescence under the influence of the gas. This setup can also be used to determine the permissible norms of air pollution for individual species of plants on the basis of the appearance of the luminescence flash.

In cities and industrial centers, sulfur dioxide acts on the green plants. Therefore, from a scientific point of view, it is important to find out whether SO_2 causes an intensification of the oxidation processes and the luminescence flash in green plants, and to determine how it affects the accumulation of luminous energy by the plant pigments. To this end, we studied the absorption of luminous energy in 5 seconds of illumination on the basis of the emission of light in the dark. When the luminescence of green plants fell to the minimum (4-5 minutes), SO_2 was used to determine the luminescence flash, as in the case of etiolated plants. After the flash had decayed, a 5-second illumination was applied again, and the binding of luminous energy was determined from the magnitude of the emission of light relative to the first light flash. The results of these studies are illustrated in Fig. 4.

It is evident from Fig. 4 that a five-second illumination causes the emission of light in the dark, strongest in the case of sprouts 6-8 days old and considerably weaker in 10-day plants. The intensity of light emission in the meadow fescue is somewhat higher than in the timothy. In the 4-8-day meadow fescue and 4-6-day timothy, 100% SO_2 causes a luminescence flash in the dark. The luminescence intensity of green plants under the influence of 100% SO_2 is much greater in the meadow fescue. Sulfur dioxide apparently causes a dissociation of the light and dark reactions of photosynthesis, and the luminous energy accumulated by the pigments is liberated, producing a luminescence flash.

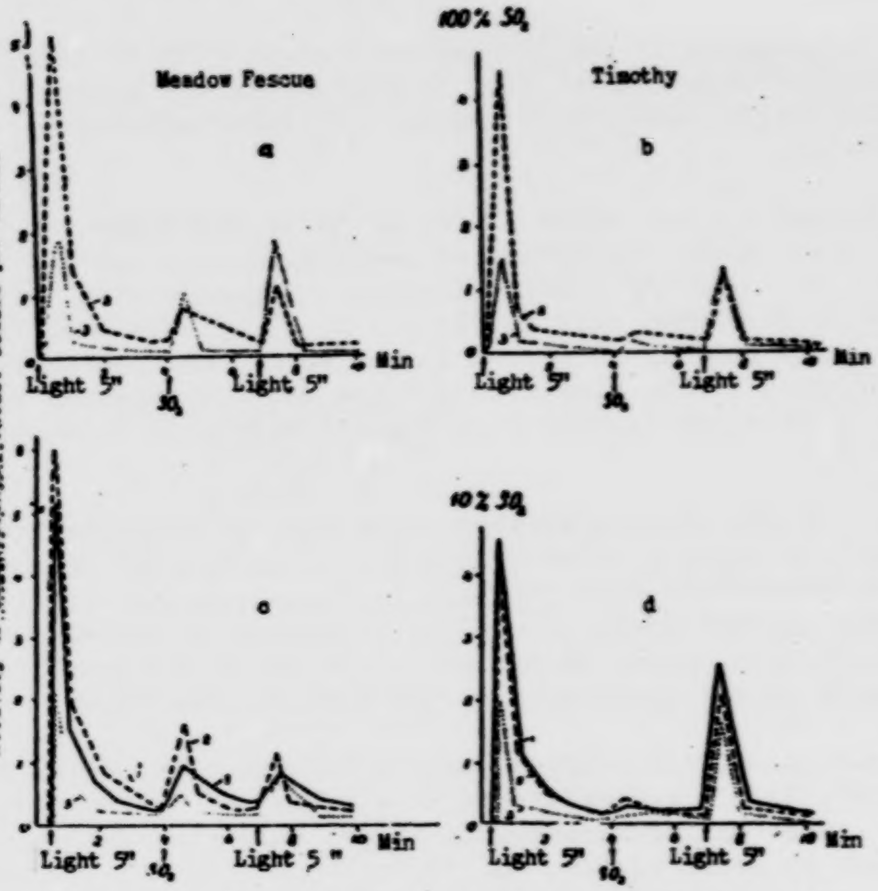

Fig. 4. (a, b, c, d). Effect of light (5 seconds) and SO_2 on the ultrafaint luminescence of green sprouts of forage grasses. Notation: a - meadow fescue - 100% SO_2; b - timothy - 100% SO_2; c - meadow fescue - 10% SO_2; d - timothy - 10% SO_2; 1 - age 6 days; 2 - 8 days; 3 - 10 days.

Subsequent irradiation of the plants with light (5 seconds) causes another flash of radiation in the dark, but it is substantially weaker (by a factor of 2-4) than the first light flash.

Thus, when the green plants are placed in the dark, they emit light. Under the influence of 100% SO_2, the green plants produce a luminescence flash in the dark, but after the action of the gas, the plants absorb less luminous energy when irradiated again. This may be attributed to an SO_2-induced inhibition of the photochemical processes by which luminous energy is bound by the plants. At the same time, the phenomenon of incomplete depression of the second luminescence flash by sulfur dioxide is only seemingly so. Luminous energy is absorbed and emitted in the dark not only by pigments, but also even by the cellulose membranes of cells. Apparently, they are the ones responsible for the second luminescence flash.

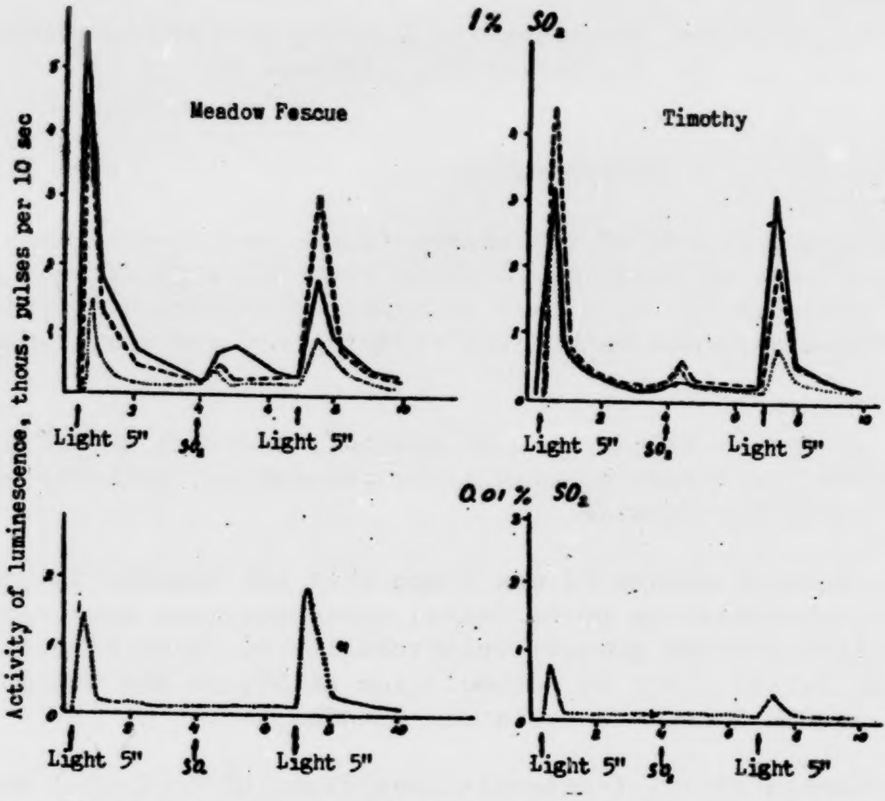

Fig. 5 (a, b, c, d). Effect of light and SO_2 on the ultrafaint luminescence of green sprouts of forage grasses.
Notation: a - meadow fescue - 1% SO_2; b - timothy - 1% SO_2; c - meadow fescue - 0.01% SO_2; d - timothy - 0.01%; 1 - age 6 days; 2 - 8 days; 3 - 10 days.

Under the influence of 10% sulfur dioxide (Fig. 4 c, d), a change in the luminescence of the plants similar to the one produced by using 100% SO_2 was observed, but in the timothy, the gas causes a fainter luminescence than in the meadow fescue. At the same time, the luminescence flash after the second irradiation with light was stronger than in the meadow fescue. This cannot be attributed to the inequality of the vegetative mass in the experiment, since the mass of the timothy was always smaller. The effect of 1% SO_2 on green plants (Fig. 5 a, b) is similar to the action of the 10% gas. Under the influence of 0.1% and 0.01% SO_2, no luminescence in the dark is observed in green plants of the meadow fescue and of timothy, and a second irradiation with light causes an even greater luminescence flash than the first flash in the meadow fescue, and it lasts longer in the timothy. Obviously, 0.1 and 0.01% SO_2 causes an increase in the binding of luminous energy by the pigments and other microstructures of the cell in green plants.

Thus, experiments with green plants showed that high sulfur dioxide concentrations (100%, 10%, 1%) cause a flash of ultrafaint luminescence which is strongest in the meadow fescue and weaker in the timothy. Lower SO_2 concentrations (0.1 and 0.01%) do not cause a luminescence flash in green plants in the dark. Concentrated gas depresses the binding of luminous energy by the plants, whereas low gas concentrations increase it.

Conclusion

Etiolated and green plants of the meadow fescue and timothy show statistically significant differences in their vulnerability to sulfur dioxide at nearly all ages (4, 6, 8, and 10 days). This makes it possible to use the biochemiluminescence method for studying the gas resistance of plants.

In etiolated and green plants of both species, a direct relationship was confirmed between the amount of oxidizable substances, ascorbic acid, and vulnerability to sulfur dioxide.

By using the isotopic method it was found that the timothy (a nonresistant species) accumulates SO_2 up to lethal concentrations more rapidly, this being responsible for the greater vulnerability of these plants. On the other hand, the lethal limit of accumulation of SO_2 in the timothy is lower than in the meadow fescue (a resistant species).

Under the influence of SO_2 (concentrations from 10% to 0.001% and lower), a luminescence flash (intensification of oxidation processes) was observed in etiolated plants. The greatest activation of luminescence and its shorter period (2-3 minutes), changing into depression, is observed at an SO_2 concentration of 10%. A lowering of the SO_2 concentration causes a decrease of the luminescence peak, but there is a simultaneous increase in the duration of the flash to 5-7 minutes.

The degree of influence of SO_2 on the ultrafaint luminescence of plants depends on their age: the greatest effect is observed at the age of greatest physiological activity (6-8), when the resistance of the plants to SO_2 is lower. One hundred percent sulfur dioxide causes a substantial depression of the luminescence of etiolated plants.

It is possible that the nature of the ultrafaint luminescence of etiolated plants under the influence of SO_2 and CO_2 is similar. Differences in the action of 100% SO_2 and CO_2 on etiolated plants result from their different chemical activities. This discovered phenomenon is proof of the nonspecific nature of the action of "acid" gases on plants.

In experiments with green plants it was found that SO_2 (concentrations of 100%, 10%, and 1%) causes a luminescence flash (intensification of oxidation processes) which is greater in the meadow fescue than in the timothy. Sulfur dioxide gas in concentrations of 0.1 and 0.01% causes no luminescence. Under the influence of SO_2, an inhibition of photochemical reactions of binding of luminous energy is observed in the former case, and in the latter case the gas causes an activation of these reactions.

The biochemiluminescence method may be used to solve problems of diagnostics of the gas resistance of plants and to determine the minimum permissible norms of air pollution for individual species of plants.

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EFFECT OF MINERAL NUTRITION ON THE METABOLISM OF CARBON-14 COMPOUNDS AND ON GAS RESISTANCE OF FORAGE GRASSES

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Because of a considerable pollution of air and soil, woody plants cannot grow at the nonferrous metallurgical plants of the Urals. Herbaceous plants are also disappearing from vast territories both in and around the plants (up to 1-2 km and more), baring the soil to erosion. Even the sowing of the hardiest herbaceous plants frequently fails to provide, there, a reliable and lasting ground cover. Increasing the gas resistance of plants by various methods will make it possible to grow greenery on such grounds and prevent their water and wind erosion.

The methods of increasing the gas resistance of plants can be arbitrarily divided into agrotechnical ones (agrotechnical cultivation and maintenance practices), chemical (regulating mineral nutrition, effect of various chemical compounds), and biological (creation of resistant cultivated phytocoenoses).

Already the first investigators (Wieler, cited by Krasinskiy, 1950; Ryabinin, 1952) indicated the possibility of indirect damage to plants by acid gases through poisoning and causing deterioration of the soil. That is why it is undoubtedly possible to increase the gas resistance of plants by regulating and improving their mineral nutrition and also through the effect obtained by means of spraying with various physiologically active and other compounds.

A number of authors (Kazantseva, 1965; Kisser, 1968; Nemec, 1958; Yatsenko, Nikolayevskiy, et al., 1968) established the positive role of nitrogen and potassium, and also of liming the soil, in the gas resistance of plants.

Attempts have been made (Bobko and Fortunatov, 1958; Guseva, 1950; Freebairn and Taylor, 1960) to increase the gas resistance of plants by means of spraying with various compounds and by means of washing off the toxic compounds from the leaves with various solvents. The mechanism of injury to plants by acid gases (Noack, 1920; Ivanov, 1936; Krasinskiy, 1950; Kroker, 1950; Nikolayevskiy, 1964) is related to a disturbance of photosynthesis in the plants.

As of this time, neither in the USSR nor in other countries, have any studies been made on the role of photosynthesis chemistry in the gas resistance of plants, or on the effect of the elements of mineral nutrition and of the physiologically active compounds on the metabolism of carbon compounds and on plant resistance. Our investigations were aimed at studying these problems in two plant species differing in their gas resistance: the meadow fescue (resistant species) and timothy (nonresistant species).

Method of Investigation

In the spring of 1967, these species were seeded on poor sandy soil. In August, after mowing, the plots (2 m x 2 m) were watered with solutions of fertilizers according to an 8-treatment scheme: control, N, P, K, NP, NK, PK, and NPK. The fertilizers were applied in the following proportions: N 4 g, P 6 g, and K 9 g per 1 m^2. On the second day (28 August) and 5th day (24 August), after watering, the effect of the fertilizers on the vulnerability of the plants to sulfur dioxide and on the metabolism of carbon-14 compounds was studied in reference to the same treatments.

The vulnerability of the plants was determined by gassing them in polyethylene chambers. Ten plants of each species in each treatment were placed in test tubes into a chamber for 1 hour, at an initial SO_2 concentration of 1/3000 by volume. The vulnerability was determined after 24 hours. It was determined as the ratio of the injured portion of the leaf to the total length of the leaf in percent. The introduction of labeled carbon dioxide ($C^{14}O_2$-1% with a specific activity of 2 μc per 1 ml) into the leaves and radiochromatographic analysis were carried out by following the procedure described by A. T. Mokronosov (1966). The activity of the samples was read off on a B-2 instrument with an SBT-7 counter. All the studies involving the use of labeled compounds were carried out at the radiochemistry laboratory of the Natural Sciences Institute of Perm' State University.

Results of Investigations

The vulnerability of the plants was determined at different times in addition to the above-indicated two days. With the age of the aftermath, the vulnerability of the meadow fescue decreased, and that of the timothy increased. This is apparently due to age-connected changes in the physiological-biochemical processes and in the gas resistance of plants during their renewed growing after mowing. Whereas at the start of the experiments (21-23 August) the fescue plants were even less resistant to SO_2 than the timothy, one observed already on 24 August that their vulnerability began to approach the indicators characteristic of adult plants. It is also possible that both in the control and in the treatments with fertilizers, the gas resistance of the forage grasses was affected by the weather conditions of that period. While a relatively dry and warm weather prevailed after the first watering with fertilizers, cloudy and cool weather prevailed after the second watering.

Data on the vulnerability of plants to sulfur dioxide and on the intensity of photosynthesis are shown in Table 1. It is apparent from the data that the meadow fescue, with the exception of the control treatment (28 August), is characterized by a lower intensity of photosynthesis than in the case of timothy. On the second day after the application of fertilizers, an increase in the resistance of the fescue was observed in treatments K, NP, and PK, and in all the treatments for timothy. On the fifth day after watering with fertilizers, a positive effect was observed in the fescue in all the treatments, and in the timothy, in all the treatments except N. No definite relationship was observed between the change in the intensity of photosynthesis (Table 1) and the vulnerability of the plants to sulfur dioxide under the influence of the fertilizers.

Statistical treatment of the data on the vulnerability of plants to sulfur dioxide showed that significant or close-to-significant differences appeared in the fescue under the influence of nitrogen and potassium, and in the timothy under the influence of K, P, and PK (24 August).

Let us consider the nature of metabolism of carbon-14 compounds in both species in the control and under the influence of fertilizers on the 2nd and 5th day after their application (Table 2).

No substantial differences were observed in the percentage distribution of the activity of C^{14} in the alcohol fraction, starch, hemicellulose and proteins in the fescue and timothy in exposures of 10" and 30" + 4.5". Some differences in the 5' exposure were observed in the content of radiocarbon in the alcohol-soluble fraction and starch: in the fescue, as compared with the timothy, the activity of the alcohol fraction is lower and higher in starch.

On the average, about 90% of carbon-14 is concentrated in the alcohol fraction (sugars, amino acids and organic acids), 3-9% in the starch, 1-4% in hemicellulose, and 0.2-2.9% in the proteins. This was also observed on the 5th day after the application of fertilizers (Table 3).

Let us consider the percent distribution (Tables 4 and 5) of the activity of carbon-14 in the forage grasses in their different groups of organic compounds (sugars, amino acids, and organic acids) and in individual products of photosynthesis under the influence of fertilizers and in relation to the change in the gas resistance of the plants. In the control plants of the fescue and timothy in cloudy weather after 10 sec of exposure, the composition of the photosynthesis products formed is nearly the same. The distribution of labeled carbon over the compounds is also similar. In the meadow

Effect of Mineral Nutrition on the Intensity of Photosynthesis

Species	Date	Intensity of Photosynthesis, Pulses per Minute					
		Control			N		
		Photosynthesis in 10 sec	Photosynthesis in 30 sec	Vulnerability % of Length	Photosynthesis in 10 sec	Photosynthesis in 30 sec	Vulnerability % of Length
Meadow	28/VIII	20490	19490	18,0	14070	14180	25,4
Fescue	2nd Day	100%	100%	100%	68,0	72,5	141,0
Timothy	28/VIII	19680	21030	27,7	27450	26440	23,0
	2nd Day	100%	100%	100%	139,0	135,0	83,0
Meadow	24/VIII	22530	44614	26,0	18724	40057	12,0
Fescue	5th Day	100%	100%	100%	83,2	90,0	46,2
Timothy	24/VIII	35147	55918	38,0	43100	54152	38,0
	5th Day	100%	100%	100%	122,0	98,2	100,0

fescue, after a 5-minute exposure (30" $C^{14}O_2$ + 4.5' light) the synthesis of sugars increases by a factor of 2.5, that of amino acids by a factor of 2, and that of the synthesis of organic acids decreases by a factor of 2. In the timothy, after a 5-minute exposure, the relative participation of C^{14} is almost completely preserved in the same compounds as in the case of the 10 sec exposure. In hot, sunny weather (24 August - Table 3), the percentage of labeled carbon in sugars was greater in the case of timothy, while in amino acids and in the organic acids, it was greater in the case of meadow fescue.

Hence, the SO_2-resistant meadow fescue in cloudy weather is characterized by a more homogeneous distribution of C^{14} in the products of photosynthesis than in the case of timothy. In the presence of increased solar radiation, the fescue is characterized by an increased incorporation of C^{14} in PGA, and in the case of the timothy, in sucrose.

Under the influence of fertilizers (Table 4), on the second day following their application, a substantial change was observed in the chemistry of photosynthesis in both species; this may be related to the change in the gas resistance of the plants. In the meadow fescue, definite changes in the metabolism of carbon-14 were caused by K, NP, PK, and NPK, and in the timothy, by all the treatments.

In the meadow fescue under the influence of nitrogen on the second day (Table 4), there was an increase in the vulnerability of the plants to sulfur

Table 1

and the Vulnerability of Forage Grasses to Sulfur Dioxide.

K			NP			PK			NPK		
Photosynthesis in 10 sec	Photosynthesis in 30 sec	Vulnerability % of Length	Photosynthesis in 10 sec	Photosynthesis in 30 sec	Vulnerability % of Length	Photosynthesis in 10 sec	Photosynthesis in 30 sec	Vulnerability % of Length	Photosynthesis in 10 sec	Photosynthesis in 70 sec	Vulnerability % of Length
15320	20480	4,6	15260	21150	4,8	13360	19810	3,1	18480	21190	22,0
75,0	108,0	26,0	61,5	109,0	26,6	65,3	101	17,2	90,0	109,0	123,0
21030	24360	23,0	22170	26900	22,3	17310	21440	9,7	25540	19770	23,6
107,0	115,0	83	113,0	127,0	81,0	90.0	102	35,0	130,0	93,5	85,5
15322	36529	15,0	20991	24843	18,0	24445	15067	20,0	21021	32310	21,0
68,0	81,5	57,5	93,0	56,0	69,0	108.0	34,0	77,0	92,0	72,3	81,0
52322	47657	18,0	27765	18818	20,0	22138	34309	26,0	30164	33030	6,0
148.0	85,0	47,4	78,0	33,6	53	63,0	61.0	68,0	86,0	59,0	15,8

dioxide, a substantial incorporation of C^{14} in the sugars (raffinose), and a decrease in the labeled C^{14} in the amino acids (glycine, alanine). Almost the same was observed under the influence of NPK. Here the labeled carbon was more extensively included in sucrose (5'). An increase in the gas resistance of the meadow fescue occurred on the second day after watering with K, NP, and PK (Table 4). In these treatments, the incorporation of C^{14} in the sugars of the meadow fescue increased (K - sucrose, NP - sucrose and fructose-1, 6-diphosphate, PK - sucrose), the incorporation of the labeled C^{14} in the amino acids decreased (K and PK - alanine) in the NP treatment, and the labeled C^{14} increased in glycine. At the same time, the C^{14} content of organic acid decreased.

In the timothy, the vulnerability of the plants to sulfur dioxide decreased in all the treatments under the influence of the fertilizer, particularly that of PK. As compared to the control, this treatment is characterized by an increase of the labeled C^{14} in the sugars (sucrose) and a decrease in organic acids (PGA and malic acid).

On the whole, in the case of a positive effect of the fertilizers, the meadow fescue is characterized by a more homogeneous distribution of C^{14} over the individual compounds than the timothy.

On the fifth day after the application of fertilizers (Table 5), all the treatments showed a positive effect on the increase of the gas resistance of the plants with the exception of nitrogen in timothy. In the meadow

Table 2

Distribution of Carbon-14 Activity in Forage Grasses According to Fractions Under the Influence of Fertilizers on the Second Day, 28 August 1967.

Species	Treatment	Activity of Hydrolyzates, Percent of Initial Value									
		PGA, Sugars, Amino Acids, and Organic Acids		Starch		Hemi-cellulose		Proteins		Total	
		10"	5'	10"	5'	10"	5'	10"	5'	10"	5'
Meadow Fescue	Control	87,2	86,5	5,2	9,3	3,2	1,3	2,8	2,5	99,0	99,6
	N	90,1	87,0	5,7	7,7	0,96	1,0	2,5	3,7	99,26	99,4
	K	91,0	95,0	6,2	—	0,7	—	2,2	4,75	100	99,75
	NP	90,8	85,0	3,6	9,7	3,2	2,8	1,4	2,0	99,0	99,5
	PK	89,0	86,0	4,1	7,8	3,1	1,3	3,5	4,2	99,7	99,3
	NPK	93,5	79,0	4,0	11,7	0,4	2,05	1,5	5,7	99,4	98,45
Timothy	Control	92,7	88,5	3,0	7,5	1,2	0,75	2,75	2,2	99,65	98,95
	N	92,5	91,5	3,26	5,5	0,8	0,6	2,5	2,3	99,16	99,9
	K	87,0	89,2	6,3	6,5	1,8	1,7	4,05	2,3	99,15	100,4
	NP	93,2	91,9	2,2	3,65	2,1	1,8	1,7	2,3	99,2	99,65
	PK	91,3	87,6	4,8	5,4	1,1	2,3	2,3	4,1	99,5	99,4
	NPK	90,2	89,0	4,5	5,8	1,6	1,2	3,1	3,4	99,4	99,4

fescue, the greatest positive effect on the gas resistance of the plants was produced by N and K, and in the timothy, by K and NPK. In these cases, in the fescue we observed (Table 5) an increase of the labeled C^{14} in the sugars (raffinose), a decrease of C^{14} in the amino acids (α- and β- alanine), and the preservation of the relative activity of organic acids. In the timothy, potassium and NPK caused a decrease of labeled carbon in the sugars and an increase in the amino acids (5' exposure) and organic acids.

Thus, in the presence of increased solar radiation (24 August), on the fifth day after the watering, the role of the fertilizers in the gas resistance of the plants and their influence on the metabolism of carbon-14 were different than in cloudy weather (28 August). The relationship between the gas resistance of the plants and the chemistry of photosynthesis can be understood if one considers the weather conditions on the days of the experiment. The difference in the chemistry of photosynthesis in the plants (control treatment) is manifested most clearly during hot, sunny weather.

Table 3

Distribution of Carbon-14 Activity in Forage Grasses on the Fifth Day After Application of Fertilizers.

Species	Treatment	Activity of Hydrolyzates, Percent of Initial Value									
		PGA, Sugars, Amino Acids, and Organic Acids		Starch		Hemi-cellulose		Proteins		Total	
		10"	5'	10"	5'	10"	5'	10"	5'	10"	5'
Meadow Fescue	Control	—	90,2	—	3,05	—	3,16	—	3,65	—	98,86
	N	92,5	90,0	3,3	4,67	1,5	1,6	2,0	2,8	99,3	99,07
	K	93,0	90,9	1,6	5,5	1,6	0,9	3,0	2,1	99,2	99,4
	NP	91,7	89,0	1,7	6,0	2,0	2,55	1,9	1,7	97,3	99,25
	PK	91,3	89,5	2,9	6,8	3,05	0,53	2,15	2,9	99,4	99,73
	NPK	87,0	89,2	5,25	4,7	4,7	3,2	2,06	2,5	99,0	99,3
Timothy	Control	88,8	87,0	5,7	5,6	2,0	3,9	0,2	2,7	96,7	99,2
	N	93,0	93,6	—	4,0	—	2,1	—	2,6	—	102,3
	K	92,2	92,1	0,27	3,6	3,3	2,2	3,9	1,5	99,67	99,3
	NP	91,8	91,7	—	3,7	—	0,9	—	2,7	—	99,0
	PK	92,1	92,7	3,95	1,6	1,0	2,05	2,15	2,6	99,2	98,85
	NPK	91,8	91,2	2,3	4,0	1,7	2,3	3,6	2,95	99,4	100,45

Under these conditions (5' exposure), the fescue is characterized (Table 5) by an increased formation of organic acids - 66% and a comparatively slight formation of amino acids and sugars (13-14%). In timothy, on the other hand, there is an increased synthesis of sugars (79.7%) and a very slight formation of amino acids and organic acids (7-12%). At the same time, the increase in the gas resistance of the meadow fescue is associated with an enhanced synthesis of sugars and a decrease in the synthesis of amino acids and organic acids, whereas in the timothy, it is due to an increase in the synthesis of amino acids and acids of the Krebs cycle.

Earlier we observed (Nikolayevskiy, 1968) that in plants resistant to SO_2 (box elder, summer-cypress), under the influence of the gas and light, the role of the pentose phosphate by-pass in respiration increases, whereas in nonresistant species (white birch, balsam poplar) the role of the Krebs cycle increases in respiration. Thus, data on the role of oxidation systems in the respiration of plants and on the chemistry of photosynthesis (Table 5)

Metabolism of Carbon-14 Compounds in Forage Grasses on the Second Day

Species and Treatments	Exposure	Initial Activity of Starting Spot (parel. samples)	Distribution of Carbon-14 Over Individual					
			Sugars					Amino
			Fructose-1, 6-Diphos-phate	Raffinose	Sucrose	Fructose	Total	Glycine
Timothy, control	10"	708	3,6	5,3	7,7	2,4	19,0	7,2
» » »	5'	624	9,4	6.9	25,8	3,9	46,0	7,9
» » N	10"	847	3,2	3,5	12,0	0,3	19,0	6.4
» » N	5'	1222	1,5	32,0	17,6	3,5	54.6	3,4
» » K	10"	702	26,7	9,0	6,4	6,0	48.1	4.2
» » K	5'	837	2,4	—	62,0	3,6	68,0	5,5
» » NP	10"	593	4,9	1,5	7,4	—	13,8	3,3
» » NP	5'	913	14,9	7,5	32,5	3,3	58,2	19,3
» » PK	10"	1215	5.8	2.6	9,2	9,8	27.4	4,4
» » PK	5'	244	—	7.7	36,5	—	44,2	9,6
» » NPK	10"	570	8.5	6.7	7,4	—	22,6	7,5
» » NPK	5'	888	1.0	8,8	57,8	2,1	69,7	4,2
Meadow fescue, control	10"	782	7,9	6,7	6,0	—	15,6	—
» » »	5'	909	3,6	—	14,0	7,2	24,8	1.8
» » N	10"	1380	7.9	0.7	13,1	—	21,7	30,4
» » N	5'	1438	2.7	1,8	54,6	—	59,1	5,8
» » K	10"	597	1,9	—	5,1	—	7,0	10,0
» » K	5'	917	1,6	1,6	53,4	—	56,6	6,2
» » NP	10"	913	2.7	8,9	15,1	3,6	30,3	5,4
» » NP	5'	1426	0.9	1,3	53,0	4,0	59,2	4,6
» » PK	10"	244	1,7	2.8	54,2	2,8	61,5	2,8
» » PK	5'	474	8,2	4,8	33,8	4,0	50,8	6,5
» » NPK	10"	966	4,1	4.1	3,1	—	11,3	12,3
» » NPK	5'	1117	7,6	1,9	48,1	3.8	61,4	8,3

Table 4

After the Application of Fertilizers (28 August 1967)

Compounds and Classes; Percent of Activity of Starting Spot											Vulnerability
Acids			Organic Acids								
α-alanine	β-alanine	Total	PGA	Citric Acid	Malic Acid	Tartaric Acid	Pyruvate	Total	Residue in Starting Spot	Total	
4,7	—	11,9	50,5	6,6	2,4	2,4	—	61,9	7,2	100	18,0
10,9	5,5	24,3	9,4	8,6	9,2	—	—	29,8	2,5	100	
6,4	—	12,8	19,0	39,3	—	5,2	—	63,5	4,7	100	25,4
6,2	—	9,6	14,6	10,6	2,0	2,4	—	29,6	6,2	100	
4,9	3,0	12,1	23,3	4,9	6,4	—	—	34,6	5,2	100	4,6
4,8	—	10,3	7,2	3,4	3,4	3,0	2,4	20,1	1,6	100	
5,8	3,9	13,2	37,0	6,2	6,7	—	—	49,0	24,2	100	4,8
5,3	2,0	26,0	10,8	2,4	—	—	—	13,2	2,0	10	
9,2	24,6	38,2	19,9	4,4	4,0	—	—	28,2	6,2	100	3,1
3,9	—	13,5	17,4	5,7	—	—	—	23,1	19,2	100	
14,7	—	22,2	33,5	3,2	2,1	8,6	1,6	49,0	6,2	100	22,0
1 6	—	5,8	8,5	5,8	6,0	—	—	20,3	4,2	100	
8,9	3,7	12,6	48,8	8,9	6,7	—	—	64,4	7,4	100	27,7
6 6	—	8,4	41,1	5,4	7,7	—	—	54,2	12,6	100	
9 0	—	39,4	25,8	5,5	2,1	—	—	33,4	5,5	100	23,0
4,4	4,0	14,2	11,6	4,4	6,3	—	1,8	24,1	2,6	100	
10,5	1,9	22,4	23,6	20,0	7,6		—	51,2	19,4	100	23,0
7,2	—	13,4	13,1	6,3	—	—	7,3	26,7	3,3	100	
14,3	—	19,7	19,6	6,2	9,8	5,4	—	41,0	9,0	100	22,3
4,0	2,6	11,2	13,2	5,1	6,0	—	2,6	26,9	2,7	100	
2,8	—	5,6	13,1	3,9	10,3	—	—	27,3	5,6	100	9,7
3,2	—	9,7	21,8	7,4	1,6	—	2,4	33,2	6,3	100	
1,1	—	13,4	30,7	19,2	3,2	—	—	53,1	22,2	100	23,6
10,2	—	18,5	15,9	1,4	—	—	—	17,3	2,8	100	

Metabolism of Carbon-14 Compounds in Forage Grasses on the

Species and Treatments	Exposure	Initial Activity of Starting Spot, pulses/min.	Distribution of Carbon-14 Over Indi-			
			Sug-			
			Fructose-1, 6-Diphosphate	Raffinosa	Sucrose	Fructose
Meadow Fescue Control	10″	—				
» »Control	5′	1831	—	4,3	10,0	—
» » N	10″	1694	—	—	11,1	—
» » N	5′	2822	2,0	25,0	3,4	0,4
» » K	10″	1628	3,0	37,5	19,4	5,0
» » K	5′	—	—	—	—	—
» » NP	10″	1590	7,0	2,4	15,2	1,6
» » NP	5′	3093	—	—	68,5	1,3
» » PK	10″	2242	0,7	1,9	9,9	—
» » PK	5′	1876	—	—	61,2	3,4
» » NPK	5′	2562	1,9	1,7	55,5	1,3
» » NPK	10″	1798	9,8	25,5	9,5	6,0
Timothy Control	10″	3504	3,0	—	36,4	—
» »Control	5′	5876	0,1	1,2	76,8	1,6
» » N	10″	3446	2,9	1,0	11,7	2,1
» » N	5′	1402	—	—	20,7	—
» » K	10″	5333	—	—	66,8	2,5
» » K	5′	1981	0,4	0,4	66,7	3,3
» » PK	10″	2121	—	—	12,4	2,1
» » PK	5′	4033	—	—	33,1	4,5
» » NPK	10″	3152	—	—	6,5	—
» » NPK	5′	2511	—	—	57,5	3,0

in relation to gas resistance yield a pattern similar to that of the dependence of plant resistance to SO_2 on the chemistry of the oxidation-reduction processes of photosynthesis and respiration. Our data attest to an interlinking and intimate coordination of metabolism which determine the resistance of the plants.

The resistance of the aftermath of forage grasses to sulfur dioxide changes with age. In the meadow fescue, this resistance is very low at the start of the regrowth and high after the regrowth is completed. In timothy, on the contrary, the resistance is high at the start and low at the end of the regrowth period.

Table 5

Fifth Day After Application of Fertilizers (24 August 1967).

vidual Compounds and Classes, % of Activity of Starting Spot											
ars	Amino Acids				Organic Acids				Residue in Starting Spot	Total	Vulnerability
Total	Glycine	α-alanine	β-alanine	Total	PGA	Citric Acid	Malic Acid	Total			
14,3	3,3	9,8	—	13,1	66,0	—	—	66,0	6,6	100	26,0
11,1	—	13,4	3,2	16,6	62,1	2,9	5,5	70,5	1,8	100	12,0
30,7	0,15	0,13	0,1	0,55	68,0	—	—	68,0	0,75	100	
64,9	—	1,0	—	1,0	34,1	—	—	34,1	—	100	15,0
—	—	—	—	—	—	—	—	—	—	—	
26,2	3,4	15,8	24,8	44,0	26,7	1,1	—	27,8	2,0	100	18,0
69,8	6,4	6,9	—	13,3	11,6	2.0	2.4	16,0	0,9	100	
12,5	3,8	4,6	—	8,4	66,3	—	—	66,3	12,8	100	20,0
64,6	2,7	13,6	—	15,3	8,4	0,7	1,6	10,7	8,4	100	
60,4	8,1	7,0	5,4	20,5	14,4	1,8	1,6	17,8	1,3	100	21,0
50,8	1,1	1,9	1,8	4,8	42,4	—	—	42,4	2,0	100	
39,4	6,8	9,6	—	16,4	27,2	10.9	4,8	42,9	1,4	100	38,0
79,7	4,3	2,9	—	7,2	8,2	1.2	3.1	12,5	0,6	100	
17,7	4,8	5,2	—	10,8	60,7	0,2	1,4	62,3	10	100	38,0
69,3	7,0	6,7	—	13,7	9,4	3,1	—	12,5	4,5	100	
20,7	3,6	6,5	2,6	12,7	54,9	2,3	2,1	59,7	7,3	100	18,0
70,8	9,2	5,9	3,3	18,4	8,8	—	1,9	10,7	0,1	100	
14,5	5.9	19,9	1,7	27,5	49,6	2,1	—	51,7	6,3	100	26,0
37,6	7,5	9.7	30,3	47,5	11,1	1,5	2.0	14.6	0.3	100	
6,5	—	5,5	—	5,5	77,8	2,7	1,6	82,1	5,9	100	6,0
60,5	—	8,3	7,6	15,9	15,2	2.3	5,6	23,1	0,5	100	

Different fertilizer treatments had a positive influence on the gas resistance of the forage grasses. At the same time, the positive effect of the fertilizers depends on the weather conditions.

The nonresistant species, timothy, has a higher intensity of photosynthesis than the meadow fescue (the resistant species).

A similar relationship between the gas resistance and a reduced intensity of photosynthesis was first noted in woody plants by V. S. Nikolayevskiy (1963).

Conclusions

The control plants of meadow fescue and of timothy after a 10-second and 5-minute exposure to $C^{14}O_2$ show practically no differences in the nature of metabolism of the main groups of organic compounds. Under the influence of fertilizers, during a five-minute exposure with $C^{14}O_2$, the polymerization rate of carbohydrates is somewhat higher in the fescue than in the timothy: the percentage of the labeled carbon is higher in the starch and lower in sucrose.

Fertilizer treatments with a positive effect on the gas resistance of plants cause different and serious changes in the synthesis of individual products. The change in the chemistry of photosynthesis may be attributed both to the indirect effect of fertilizers and periods following their application, and to the species characteristics and the effect of weather conditions. In the meadow fescue, in the presence of increased solar radiation, the improvement in gas resistance under the influence of fertilizers is associated with an increase in synthesis of sugars and a reduction in the synthesis of amino acids and organic acids; on the contrary, in the timothy, an increase of the synthesis of the latter compounds is observed.

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METABOLISM OF CARBON-14 COMPOUNDS IN FORAGE GRASSES AND THE EFFECT OF SULFUR DIOXIDE ON IT

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At the start of the 20th century, physiological-biochemical methods became increasingly popular in studies of the gas resistance of plants. They were used to reveal the characteristic physiological-biochemical peculiarities of plants in connection with differences in gas resistance (Krasinskiy, 1950; Kroker, 1950; Nikolayevskiy, 1964; Kazantseva, 1965; Sitnikova, 1966; Kulagin, 1965, 1966; Il'kun and Motruk, 1968; Kisser, 1968). On the other hand, many of the established indicators of plant gas resistance ("oxidizability," water-holding capacity, ascorbic acid content, etc.) apparently are not directly related to gas resistance. More often than not, they are merely indirect reflections of differences in the vital activity and gas resistance of plants. Considering the general biological importance of the proteins and biocolloids of the protoplasm, and the importance of the metabolism of organic compounds in the regulation of the life processes of various biosystems (cell, organism, population), one can assume their important role in plant gas resistance as well.

The development of new isotopic methods of studying the metabolism of organic compounds - radiochromatography (Arnon, 1959; Mokronosov, 1966) - made it possible to initiate more refined biochemical studies of plant gas resistance (M. D. Thomas et al., 1944 a, b; Harrison et al., 1944; Godzik, 1968). Still, differences in the nature of the metabolism of organic compounds in plants differing in gas resistance, conversion and detoxication* of acid gases by the plant, and change and disturbance of the processes of photosynthesis and respiration under the influence of gases are still unclear. We attempted to study the chemistry of photosynthesis in two species of forage grasses of different gas resistance, namely: that of the meadow fescue (a resistant species) and of the timothy grass (a nonresistant species).

Procedure

Plants for the experiments were grown in pots on fertile soil. The photosynthesis and the effect of sulfur dioxide on it were studied on cut plants 20 and 30 days old with the help of labeled carbon dioxide (1% $C^{14}O_2$, specific activity 2 µC per ml). The introduction of $C^{14}O_2$ into the leaves and the radiochromatography of organic compounds were performed according to a method described by A. T. Mokronosov (1966). Sulfur dioxide ($S^{35}O_2$) with a specific activity of 10 µC in 1 ℓ was introduced by fumigating the plants in polyethylene chambers. The vulnerability was determined as the ratio of the damaged length of the leaf to the total length, expressed in percent. The activity of the plant samples was read on a B-2 instrument with an SBT-7 counter at a voltage of 380 volts.

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* [Translator's note: "intoxication" in Russian original.]

The amount of substances oxidizable by a 0.1 N solution of $KMnO_4$ was determined by N. P. Krasinskiy's procedure (1950), the determination of ascorbic acid content according to the method of Ye. V. Sapozhkova (1966), and of the total acidity, by the methods of A. Ye. Yermakov, V. V. Arasimovich, and others (1952).

Experiments dealing with the study on the metabolism of carbon-14 and sulfur-35 compounds were carried out in the following variants:

1. The plants were fumigated with sulfur dioxide ($S^{35}O_2$) for 10 minutes and 1 hour. The fixation of the material was carried out with ethanol vapor (for 3 minutes) after the fumigation and after 24 and 72 hours.

2. On the control and experimental plants (from the preceding variant), photosynthesis was studied in a 100 ml chamber closed with mercury (Mokronosov, 1966). The exposures were 15_{sec} $C^{14}O_2$, 1_{min} $C^{14}O_2$, and 1_{min} $C^{14}O_2+4_{min}$ light.

3. Sulfur dioxide ($S^{35}O_2$) was introduced into the cut plants in the same photosynthesis chamber from a gas-washing bottle connected in parallel. After SO_2, $C^{14}O_2$ was introduced into the chamber. Sulfur dioxide - 14% with a specific activity of 8.3 µC per ml, $C^{14}O_2$ - 1%, specific activity 2 µC per ml.

4. In the last variant, the photosynthesis was studied in a mixture of 1% $S^{35}O_2$ and 1% $C^{14}O_2$ for 5 and 15 seconds and 1, 5, and 10 minutes. The specific activity of $S^{35}O_2$ was 5.5 µC per ml, and that of $C^{14}O_2$, 2 µC per ml.

Studies using isotopes of carbon and sulfur were carried out in the radiochemistry laboratory of the Natural Sciences Institute of Perm' State University. The authors express their gratitude to V. Ye. Zhuravlev and the laboratory staff for their cooperation in these studies.

Results of Investigation

In order to select the objects for the study of gas resistance, we first tested 20-day old green sprouts of 9 species of plants (Table 1).

It is evident from Table 1 that among the forage grasses, the lowest vulnerability to gas injury is displayed by the meadow fescue, and the highest by the timothy grass. Differences in the vulnerability of these species were statistically significant in all five experiments.

Table 1

Vulnerability of Plants to Sulfur Dioxide

Species	Percent Damage to Length of Leaf
1. Meadow fescue	2.0
2. English ryegrass	6.0
3. Orchardgrass	9.8
4. Pasture ryegrass	15.5
5. Creeping wheatgrass	20.0
6. Awnless bromegrass	23.0
7. Meadow foxtail	26.0
8. Timothy grass	38.0
9. Red clover	100.0

In the case of the fescue and timothy plants studies were made as to the content of their oxidizable substances, ascorbic acid, and organic acids, as well as on the effect of sulfur dioxide (Table 2).

The species differing in gas resistance - fescue and timothy - possess certain biochemical characteristics (Table 2). The resistant species (meadow fescue) is characterized by a reduced content of substances oxidizable by potassium permanganate, a reduced ascorbic acid content, and a lower total acidity. Under the influence of sulfur dioxide an increase in the content of oxidizable substances takes place, in contrast to Krasinskiy's data (1950). It may be postulated that the change in the content of these compounds also depends on the time elapsed after the beginning of the effect of sulfur dioxide. During the first few hours, the latter apparently causes depolymerization and an increase in the amount of oxidizable substances. As time goes on, more extensive processes of oxidation and outflow of organic compounds produce a decrease in the amount of oxidizable substances.

The ascorbic acid content decreases under the influence of SO_2 (Table 2). This is particularly obvious in the calculation per gram of dry weight. The decomposition of ascorbic acid under the influence of SO_2 is more marked in the nonresistant species - timothy, and less marked in the fescue. As is evident from Table 2, a more precise and reliable indicator of gas resistance and of the effect of sulfur dioxide on plants is the ascorbic acid content.

Table 2

Some Biochemical Characteristics of Forage Grasses and the Effect of Sulfur Dioxide on Grasses

Species	Age of Plants	Vulnerability of Plants, %	Control							Experiment						
			Amount of Substances oxidizable by 0.1 N $KMnO_4$ in 1 g of green weight			Ascorbic Acid Content, mg %		Total Content of organic acids in percent of malic acid		Amount of Substances oxidizable by 0.1 N $KMnO_4$ in 1 g of green weight			Ascorbic Acid Content, mg %		Total Content of organic acids in percent of malic acid	
			Water-Soluble Fraction	Water-Insoluble Fraction	Total Content	Per g of Green Weight	Per g of Dry Weight	Per g of Green Weight	Per g of Dry Weight	Water-Soluble Fraction	Water-Insoluble Fraction	Total Content	Per g of Green Weight	Per g of Dry Weight	Per g of Green Weight	Per g of Dry Weight
Meadow fescue	20 days	9.7	0.95	1.75	2.65	4.6	7.0	0.022	0.33	0.55	1.30	2.15	4.6	4.0	0.069	0.53
Timothy grass	20 days	48.4	0.85	1.90	2.75	5.3	6.2	0.029	0.33	0.70	2.40	3.10	3.7	2.5	0.028	0.25
Meadow fescue	30 days	17.5	0.50	0.90	1.40	2.7	3.4	0.020	0.26	0.55	1.00	1.55	2.5	2.1	0.024	0.21
Timothy grass	30 days	50.8	0.90	1.55	2.45	3.4	4.2	0.026	0.22	1.20	2.30	3.50	3.0	1.7	0.039	0.22

Comparison of the intensity of photosynthesis in the plants (Table 3) shows that for all exposures, the rate of carbon dioxide absorption in the meadow fescue, in comparison with timothy grass, is lower by an average factor of 1.5. This confirms our conclusion (Nikolayevskiy, 1963) that the intensity of photosynthesis is lower in the resistant species.

Table 3

Intensity of Photosynthesis in Forage Grasses, Pulses per min (200 mg of Dry Weight)

Species	Exposure		
	15 sec $C^{14}O_2$	1 min $C^{14}O_2$	1 min $C^{14}O_2$ + 4 min light
Meadow fescue	2025	6052	7011
Timothy grass	5630	9015	13353

The absorption and redistribution of $S^{35}O_2$ by the plants (Table 4) showed that the build-up of $S^{35}O_2$ in the fescue continues for the duration of 30-50 minutes, whereas in the timothy, the build-up takes place only during the first 10 minutes. During the first 10 minutes of the experiment, the timothy accumulates per gram of dry weight three times as much toxic gas as the fescue. Even in long exposures, the amount of absorbed sulfur dioxide in the timothy is greater than in the fescue. The rate of outflow of toxic compounds for 10 minutes was 3-5% of the accumulated amount.

Short periods of gassing and low $S^{35}O_2$ concentrations activate the photosynthesis (absorption of $C^{14}O_2$), whereas higher concentrations of the gas and longer exposures to it cause a decrease in the intensity of photosynthesis.

Table 4

Absorption of Sulfur Dioxide by The Plants, Pulses per Min (1 g of Dry Weight)

Species	Exposure to $S^{35}O_2$				
	10 min	10 min + 23 hr up to fixation	1 hr	1 hr + 23 hr up to fixation	1 hr + 72 hr up to fixation
Meadow fescue	48630	45300	115730	122950	112600
Timothy grass	166800	156350	166043	—	—

Sulfur dioxide absorbed by the plants undergoes various chemical transformations. According to M. D. Thomas, R. H. Hendricks, G. R. Hill (1944), Kroker (1950), and Yang and Mou (1961), SO_2 in the plants is oxidized to sulfate (SO_4) and is partially utilized in the synthesis of amino acids and proteins. Our experiments (Table 5) showed that in the fescue up to 88% and in the timothy up to 95% of the labeled sulfur is contained in the alcohol- soluble fraction, only slight amounts being present in starch, hemicellulose, proteins, and cellulose. It may be assumed that in the latter compounds sulfur is tied not chemically, but by adsorption and electrostatic forces.

Chromatography of the alcohol-soluble fraction in the system phenol-water (80:20) and butanol - formic acid - water (75:13:12) showed that the labled sulfur remains almost entirely in the starting spot. Slight indications of the advancement of the sulfur with monosaccharides were noted only in the fescue. Since these forage grasses, when subjected to short-duration exposures, showed no sulfur-containing compounds in any of their organic products formed during photosynthesis, one may assume as well that in the alcohol-soluble fraction, the sulfur is adsorbed on different organic substances. It is also possible that a certain insignificant amount of sulfur enters into the composition of readily water- and alcohol-soluble proteins and their amino acids (cystine, methionine).

Since the incorporation of C^{14} into the indicated groups of organic compounds in the forage grasses is similar, we shall consider the differences in the metabolism of individual compounds (Table 6). In short exposures of the fescue the labeled carbon is concentrated in fructose-1, 6-diphosphate, sucrose, alanine, and citric acid. In long exposures (1' + 4'), the labeled carbon also appears in all the other compounds. In the timothy, the labeled carbon concentrates in the sugars and alanine even in long exposures. Thus, forage grasses which differ in gas resistance also differ in the nature of the metabolism of organic compounds.

The resistant species (meadow fescue) is characterized by a high rate of synthesis of various organic compounds at a comparatively low absorption rate of $C^{14}O_2$. The nonresistant species (timothy) is characterized by a high intensity of gaseous exchange and low rate of transformation of organic compounds. If we are to imagine that instead of CO_2 the plants will assimilate SO_2, as is sometimes the case at industrial enterprises, then the role of the chemical processes of photosynthesis in the gas resistance of plants becomes understandable. The oxidation of the anion SO_2 to the sulfate proceeds faster in the meadow fescue than in the timothy, thus decreasing the toxicity of the sulfate. On the other hand, the great variety of the photosynthesis products (a more limited specialization of metabolism, according to A. V. Blagoveshchenskiy, 1950) apparently plays an important part in blocking the noxious action of sulfur dioxide.

Since labeled sulfur is not incorporated into any of the organic compounds, in which carbon is incorporated at the same exposures, the data of Table 6 on the activity of the products of metabolism in variants involving

$S^{35}O_2$ can be attributed only to the incorporation of carbon C^{14} in them.

Table 5

Results of General Radiochemical Analysis of the Distribution of Sulfur in Plants

Experimental Conditions	Distribution of $S^{35}O_2$ over groups of organic compounds %						
	Initial Activity in 1 g. of dry weight	Alcohol Fraction	Starch	Hemicellulose	Proteins	Cellular Tissue	Total Content
		Meadow Fescue					
10 min $S^{35}O_2$	48650	84,7	4,1	5,4	4,1	1,5	99,8
1 hr $S^{35}O_2$	118905	84,7	1,9	6,5	3,6	0,9	97,6
1 hr $S^{35}O_2$ +23 hr	122950	88,2	2,4	2,8	5,1	1,1	100
		Timothy Grass					
10 min $S^{35}O_2$	166800	84,1	5,3	2,7	7,1	0,9	99,8
10 min $S^{35}O_2$ +23 hr	156350	94,9	1,4	0,9	2,7	0	99,9
1 hr $S^{35}O_2$	166043	93,3	—	—	—	—	

Under the influence of short exposures to SO_2 (15" $S^{35}O_2$ + 1' $C^{14}O_2$), the synthesis of complex sugars (sucrose, raffinose) and alanine is retarded in the meadow fescue. In the meadow fescue, under the influence of long exposures to SO_2 (5' $S^{35}O_2$ + 1' $C^{14}O_2$), the synthesis of glucose, fructose, raffinose, and asparagine is intensified, whereas that of sucrose, α-alanine and citric acid is reduced. In the variant with an additional four-minute illumination, a decrease in the activity of C^{14} is observed in glucose, fructose, and particularly sucrose and β-alanine (Table 6). Thus, despite the action of sulfur dioxide, the synthesis of all the organic compounds is preserved in the fescue.

In the timothy, a prolonged exposure to sulfur dioxide (5' $S^{35}O_2$ + 1' $C^{14}O_2$) causes more serious disturbances in the metabolism of organic compounds: the synthesis of fructose-1, 6-diphosphate, fructose, and citric acid decreases considerably, and there is an acceleration in the synthesis of glucose, sucrose (by a factor of 10), α-alanine, and malic acid. An additional four-minute illumination causes C^{14} to concentrate in sucrose. As in the control variant, the timothy synthesizes a limited number of compounds, in contrast to the meadow fescue.

Even in very long exposures to SO_2 (1 hour), the meadow fescue retains a close-to-normal metabolism of organic compounds despite the presence of visible damage.

Table 6

Metabolism of Carbon C^{14} Compounds in Forage Grasses

Species	Exposure	Distribution of C^{14} Over Individual Compounds, Percent										
		Starting Spot	Fructose-1,6-Di-phosphate	Glucose	Fructose	Sucrose	Raffinose	Asparagine	α-alanine	β-ananine	Citric Acid	Malic Acid	Total Content
Meadow fescue	$15''C^{14}O_2$	3,5	30,0	—	—	17,2	—	—	34,0	—	15,3	—	100
Meadow fescue	$1'C^{14}O_2$	1,6	32,7	—	1,9	42,5	—	—	18,4	—	2,9	—	100
Meadow fescue	$1'C^{14}O_2+4'$ light	11,0	41,9	1,0	3,3	18,9	6,0	1,8	13,9	—	1,3	0,9	100
Timothy grass	$1'C^{14}O_2$	8,1	55,6	—	11,3	2,4	—	1,5	6,3	—	14,6	—	100
Timothy grass	$1'C^{14}O_2+4'$ light	4,6	21,7	7,6	4,4	51,7	—	—	10,0	—	—	—	100
Meadow fescue	$1'S^{35}O_2+1'C^{14}O_2$	24,3	55,1	1,7	—	5,9	4,5	—	8,1	—	—	—	100
Meadow fescue	$1'S^{35}O_2+1'C^{14}O_2$	50,0	24,8	3,2	—	5,8	3,5	3,5	7.0	—	—	2,0	100
Meadow fescue	$4'$ light	21,2	43,0	—	8,5	11,4	—	—	8,0	3,4	4,5	—	100
Meadow fescue	$5'S^{35}O_2+1'C^{14}O_2$	7,2	30,0	5,9	5,3	21,0	13,6	5,6	11,4	—	—	—	100
Meadow fescue	$5'S^{35}O_2+1'C^{14}O_2+$ $+4'$ light	3,3	17,6	5.3	8,7	36,5	4,0	3,8	13,1	4,3	2,7	0,7	100
Timothy grass	$5'S^{35}O_2+1'C^{14}O_2$	14,2	45,2	3,1	3,1	20,7	—	—	10	—	—	3,7	100
Timothy grass	$5'S^{35}O_2+1'C^{14}O_2+$ $+4'$ light	12,2	30,2	—	—	44,6	—	—	9,5	—	—	3,7	100
Meadow fescue	1 hr SO_2+ $+1'C^{14}O_2$	16,7	31,1	—	5,0	6,2	4,2	5,0	28,0	—	3,6	—	100
Meadow fescue	1 hr SO_2+ $+1'C^{14}O_2+$	10,2	17,5	—	4,6	43,7	10,0	2,5	11,5	—	—	—	100

Conclusions

1. Forage grasses differing in gas resistance also differ in their content of oxidizable substances and ascorbic acid. A resistant species (meadow fescue) is characterized by a reduced content of oxidizable substances and ascorbic acid. Under the influence of SO_2, an increase in the content of oxidizable substances is sometimes observed.

2. The meadow fescue as compared with timothy is characterized by a reduced intensity of photosynthesis and a lower rate of absorption of SO_2.

3. When plants are fumigated with sublethal and lethal doses, the sulfur isotope concentrates in the alcohol-soluble fraction (up to 88-95%). A slight activity is observed in starch, hemicellulose, and proteins, and a very slight activity in cellulose.

4. Most of the sulfur accumulated in the plant appears to be in inorganic form, since it cannot be separated by paper chromatography and remains almost entirely in the starting spot.

5. The forage grasses studied differ in the nature of the metabolism of carbon C^{14} compounds under normal conditions in long exposures (5 minutes or more). The meadow fescue is characterized by a great variety of synthesizable substances (unspecialized type of exchange, according to A. V. Blagoveshchenskiy); on the other hand, the timothy synthesizes a limited number of products (spezialized type of exchange).

6. Under the influence of SO_2, definite changes in the metabolism of carbon in forage plants are observed which are attributable to their gas resistance.

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EFFECT OF SULFUR DIOXIDE ON PIGMENTS OF FORAGE GRASSES

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According to K. Noack (1920, 1925) and N. P. Krasinskiy (1950), a definite role in the injury to plant leaves by sulfur dioxide is played by pigments, which continue the absorption and accumulation of solar energy despite the discontinuation of photosynthesis. These authors explain the formation of necroses on leaves exposed to SO_2 by the development of photodynamic oxidation processes the energy for which is supplied by the pigments. Alongside the destruction of the cell content under the influence of SO_2, the pigments in the leaves are also destroyed by this gas. Acted upon by SO_2 and light, the chlorophyll in the leaves is converted into pheophytin (Jahnel, 1954; Nemec, 1958; Dorris, cited by Tomas, 1962). The decomposition products of pigments apparently also participate in the photodynamic oxidation of the cell substrate, since A. A. Krasnovskiy (1959) established that pheophytin is also capable of binding luminous energy, and G. P. Brin (1959) and V. B. Yevstigneyev (1962) showed that pheophytin is capable of sensitizing oxidation processes. Pheophytin was also found to have even a greater oxidizing effect than chlorophyll.

In order to determine the chemistry and mechanism of photodynamic oxidation processes in plants under the influence of SO_2 in light, it is important to study the influence of this gas on pigment systems. Thus far, no detailed investigations along these lines have been made in the USSR or in other countries. From very scanty literature sources (Krasinskiy, 1950; Jahnel, 1954; Spaleny, Godny, and Marzhan, 1962) it is known that under the influence of a steady action of acid gases, the chlorophyll content of plants decreases. The degree of reduction of chlorophyll is directly related to the vulnerability of the plants.

According to modern concepts (Sapozhnikov et al., 1962; Sapozhnikov, 1963; Khodzhayev, 1963), not only chlorophyll but also carotinoids participate in the absorption of luminous energy. It is assumed that carotinoids (the system lutein-violaxanthin) participate in the transfer of oxygen in one of the intermediate steps of photosynthesis.

Plant pigments act not only as acceptors of luminous energy, but also participate in the regulation of growth and development. An increase of xerophytization of leaves, reduction of growth and yield, and disturbance of the stages of development, noted by several authors (Antipov, 1957;

Nikolayevskiy, 1964; Babkina, 1968), may be due not only to a reduction of photosynthesis but also to a disturbance of the form-developing role of pigments.

The degree of resistance of plant pigments to the action of extreme factors (light, temperature, acids) depends not only on the chemical structure of the molecule, but also on the type of their bonding with the protein-lipoid complex in the plastids. In the active monomer form, chlorophyll is less resistant to the action of light and acids than in the aggregate form (A. A. Krasnovskiy, 1959).

By decreasing the pH of the protoplasm and organelles in plants, sulfur dioxide enhances the enzymatic oxidation processes (Nikolayevskiy, Suslova, 1968; Nikolayevskiy, 1968). This apparently causes the rupture of labile bonds between the pigments and the protein-lipoid complex and the formation of monomeric and even molecular forms of the pigments, causing a decrease of their resistance to light. Evidence of the above is provided by the appearance of necrotic blotches in plants under the influence of SO_2 in light, and their absence from plants in the shade (Kroker, 1950; Krasinskiy, 1950; Jahnel, 1954). In experimental studies, in order to reveal the injuries more rapidly, it is necessary that plants fumigated with sulfur dioxide always be placed in direct sunlight.

From the theoretical point of view, in order to determine the mechanism and chemistry of the SO_2 action on green plants, it is important to study the dynamics of the process of destruction of pigments and change of their photodynamic role. It is more likely that the pigments are not destroyed immediately after coming in contact with SO_2, but gradually, during the parallel effect of SO_2 and light. For this reason, necroses appear only 1 to 24 hours or more after the plants have been placed in direct light. Less likely is the hypothesis that pigments are destroyed only during the final stages of the death of cells. The elucidation of the mechanism by which chlorophyll is revived (Bazhanova et al., 1964; Shlyk, 1965) in the process of metabolism makes it necessary to assume an increase in the breakdown of pigments and an impairment of their synthesis as a function of the SO_2 concentrations, light, and time elapsed since the gassing of the plants.

Among the objectives of our investigation were those of studying (a) the resistance of individual plant pigments to acidification of the protoplasm as a result of accumulation of SO_2, and (b) the stability of the pigments as a function of the stages of growth, development, and gas resistance of the plants.

Method of Investigation

The studies were conducted on the meadow fescue (Festuca pratenis Huds) - a gas-resistant species, and timothy (Phleum pratense L.) - a nonresistant species. These forage grasses were grown at the university's botanical garden on poor sandy soil. During the tillering stage of the two species and during the booting and blooming stages of timothy, the plants were fumigated with sulfur dioxide in a 0.125 m^3 polyethylene chamber for 1 hour. The initial SO_2 concentrations (2.5×10^{-5}; 5×10^{-5}; 10^{-4}; 2×10^{-4}; 4×10^{-4} by volume) were produced by reacting an exact amount of Na_2SO_3 with sulfuric acid according to the equation

$$Na_2SO_3 + H_2SO_4 = Na_2SO_4 + SO_2 + H_2O.$$

The composition of the pigments in the experimental and in the control plants was studied immediately after the gassing, and a second time after 24 hours. The second and third leaves, counting from the top of the plant, were used for the analysis. The pigments were separated by paper chromatography according to Sapozhnikov (1964), and the quantitative determinations were made on FEK-M. The calibration curves for FEK-M were plotted by determining a series of pigment solutions on SF-4a and FEK-M. Since after the fumigation and injury of the plants with sulfur dioxide a decrease in the water content of the leaves was observed, it was necessary, in order to compare the data for the first and second days of the experiments, to determine the moisture content of the leaves and to take into account a correction for the change of the moisture content.

The vulnerability was determined by measuring the injured and total length of the leaf with a ruler. The ratio of the former to the latter (in percent) was taken as the vulnerability.

Results of Investigation

Since the meadow fescue in its first year of life goes only through the tillering stage, while the timothy goes through all the stages of growth-development up to blooming and fruiting, the pigment composition and the effect of sulfur dioxide on it were studied in the first species during the tillering stage and in the second, during the stages of tillering, booting, and blooming.

During the tillering stage (Table 1) in the meadow fescue, chlorophylls a and b account for 82.6%, carotene for 1.3%, and xanthophylls, for 16.1% of the total content of pigments in the leaves. Among the pigments entering into the composition of xanthophylls, the predominant one is lutein - 48%.

The ratio $\frac{\text{chlorophyll a}}{\text{chlorophyll b}}$ $(\frac{Xa}{Xb})$ in the meadow fescue is 4.15;

$$\frac{\text{chlorophyll a + b}}{\text{yellow pigments}} \left(\frac{Xa + b}{y.\ p.}\right) = 4.7;$$

$$\frac{\text{xanthophylls}}{\text{carotene}} \left(\frac{X.}{car.}\right) = 13.0.$$

Thus, among chlorophylls, the reduced form, chlorophyll *a*, predominates, and among yellow pigments, the oxidized forms - lutein, violaxanthin and neoxanthin are predominant.

The pigment composition of the timothy during the tillering stage is very close to that of the meadow fescue (Table 1), with the exception of the ratio $\frac{X.}{car.}$, which was found to be somewhat smaller.

Hence, forage grasses which differ in their resistance to SO_2 show no substantial differences in the pigment composition during their tillering stage.

In the timothy (Table 1), a change in the pigment composition of the leaves can be detected during its growth and development. During the booting stage as compared with the tillering stage, the amount of chlorophyll *a* decreases somewhat, and the content of chlorophyll *b* increases, the total chlorophyll content remaining the same. Thus the ratio Xa/Xb decreases to 3.6. A certain decrease also takes place in the ratio X/car. during the booting stage, because of an increase in the carotene content. At the same time, the total absolute content of pigments during the booting stage increases by 34% as compared with the tillering stage, and increases by 79% during the blooming stage.

During the blooming stage of timothy, the ratio of green pigments Xa/Xb = 4.6 is once again restored. The ratio X./car. increases to 12.6. Hence, in the timothy, a comparatively stable pigment composition is observed during the ontogeny. The ratio X./car. changes only slightly, and the ratio X a+b/y.p. remains almost unchanged.

During the tillering stage, we chose such SO_2 concentrations that it would be possible to obtain a vulnerability of 0 to 100% in both species. Subsequently, these SO_2 concentrations were also used in other stages of growth and development.

Figure 1 shows the change in the vulnerability of the meadow fescue and timothy as a function of the stages of growth, development, and gas concentrations. It is evident from Fig. 1 that during the tillering stage, the leaves of the timothy accumulate SO_2 up to lethal doses more rapidly than those of the fescue. Hence, SO_2 causes the poisoning and death of the leaf cells and tissues more rapidly in the timothy than in the meadow fescue. However, at SO_2 concentrations of 2.5×10^{-5} and 4×10^{-4}, the vulnerability of both species is similar: in the former case it is 0%, and in the latter, 92 and 93%.

As the timothy grows and develops, a regular increase in the vulnerability of leaves is observed at the same SO_2 concentrations (Fig. 1); this may be explained, on the one hand, by an increase in the lethal effect of

Table 1

Seasonal Dynamics of Pigments in Forage Grasses

Species and Stages	Amount of Pigments in mg per g of Green Weight										Ratio $\frac{xa}{xb}$	Ratio $\frac{x}{y.\,p.}$	Ratio $\frac{x}{car.}$
	Chlorophyll *a*	Chlorophyll b	Chlorophyll a + b	Carotene	Lutein	Violaxanthin	Neoxanthin	Total xanthophyllis	Total Yellow Pigments	Sum of all Pigments			
Meadow fescue tillering	1,776 66,6	0,426 16	2,202 82,6	0,036 1,30	0,208 7,8	0,127 4,7	0,096 3,6	0,431 16,1	0,467 17,4	2,669 100%	4,15	4,7	13,0
Timothy, tillering	1,226 67,9	0,266 14,6	1,492 82,5	0,033 1,7	0,129 7,2	0,080 4,3	0,08 4,3	0,289 15,8	0,322 17,5	1,814 100	4,6	4,6	8,7
Timothy, booting	1,57 64,4	0,43 17,6	2,00 82,0	0,053 2,1	0,179 7,4	0,127 5,2	0,080 3,3	0,386 15,9	0,439 18,0	2,439 100	3,65	4,55	7,3
Timothy, blooming	2,16 66,8	0,47 14,5	2,63 81,3	0,045 1,4	0,247 7,5	0,180 5,6	0,138 4,2	0,565 17,3	0,610 18,8	3,24 100	4,6	4,3	12,6

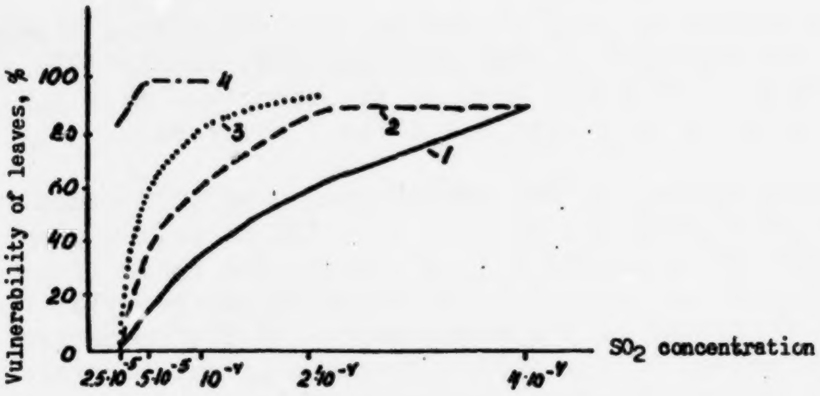

Fig. 1. Change in the vulnerability of forage grasses as a function of the stages of growth and development and concentration.
Notation: 1 - meadow fescue - tillering; 2 - timothy - tillering; 3 - timothy - booting; 4 - timothy - blooming.

the toxic gas, and on the other hand, by an increased rate of gaseous exchange and hence, a greater accumulation of SO_2 during an equal time interval. The decrease in the gas resistance of the timothy when the latter enters the stages of booting and blooming becomes understandable if one considers that an intensification of the physiological-biochemical processes takes place in the plants during these stages. Earlier, we established (Nikolayevskiy, 1964) a direct correlation between the intensity of photosynthesis and respiration in woody plants and their vulnerability to sulfur dioxide.

Let us consider the effect of SO_2 on the pigment composition of the meadow fescue according to the stages of growth and development and as a function of the gas concentration and vulnerability of the plants (Table 2). For convenience of comparison, the tables give the content of pigments in percent of the control. In the meadow fescue during the tillering stage, the lowest SO_2 concentration, 2.5×10^{-5}, caused a decrease in the content of carotene, violaxanthin, and neoxanthin on the day of the experiment. In addition, a slight increase was observed in the content of chlorophyll b and in the ratio of the different pigments to each other Xa/Xb, Xa + b/y. p. X./(car.), close to those in the control. Because of the destruction of yellow pigments, the ratio $\frac{Xa + b}{y.\ p.}$ and $\frac{X.}{car.}$ increased somewhat in the experiment.

An SO_2 concentration of 5×10^{-5} caused on the first day a decrease in carotene content and increase in the content of violaxanthin and neoxanthin. As before, an increase in the ratio X/car. was observed in this case. More pronounced changes were observed in the experimental plants on the second day.

Thus, as compared with the control plants, the content of pigments was higher, namely: chlorophyll 9-26%, carotene 55%, lutein 30%, violaxanthin 92%, and neoxanthin 132% higher than in the control. As a result, the ratios of the pigments (Xa/Xb; Xa + b/y. p.; X/car.) decreased.

In the meadow fescue, an SO_2 concentration of 10^{-4} caused a reduction of 50% in chlorophyll a and b and of more than 50% in yellow pigments. The carotene content remained unchanged. As a result, the ratio X/car. decreased to 10.8. On the second day, a certain increase in xanthophylls was observed as compared to the first day of the experiment. An SO_2 concentration of 2×10^{-4} on the first day caused in the meadow fescue a slight increase in the content of chlorophyll a and b, carotene, and neoxanthin and a decrease in the content of violaxanthin and lutein. On the second day, as in the preceding case, an increase in the content of all the pigments, particularly marked in the case of chlorophyll a and b, lutein, and neoxanthin, was observed.

The highest SO_2 concentration, 4×10^{-4}, which caused an almost complete destruction of the plants, decreased the contents of all the pigments on the first day, but on the second day an increase of their content was observed. The latter phenomenon may be explained by an increase in the extractability of the pigments as a result of hydrolysis of the proteins in the protoplasm and plastids.

Thus, in the meadow fescue during the tillering stage, the change in the content of pigments stands in some direct relationship to the SO_2 concentration. The yellow pigments are destroyed more rapidly and more severely under the influence of SO_2, and among these, carotene is destroyed at a particularly rapid rate.

On the second day after the action of SO_2, an increase in the content of pigments was observed in the meadow fescue. The increase in the content of chlorophyll b, lutein and neoxanthin was more pronounced. The carotene content at low SO_2 concentrations also increased, and at high concentrations remained unchanged on the second day. Under the influence of SO_2, the appearance of pheophytin was observed in the plants as indicated by the chromatograms.

In the timothy during the tillering stage, the first SO_2 concentration, 2.5×10^{-5}, caused a substantial destruction of chlorophyll a and b and a certain decrease in lutein and increase in neoxanthin content on the first day of the experiment. The ratio Xa + b/y. p. decreased. In the timothy, on the first day, the 5×10^{-5} SO_2 concentration caused a decrease in the content of chlorophyll a, lutein, and neoxanthin, and an increase in the content of chlorophyll b and violaxanthin. On the second day, the reduction in the content of chlorophyll a and b continued, and the lutein content increased.

In the timothy, the 10^{-4} SO_2 concentration caused a destruction of chlorophyll b, lutein, as well as of neoxanthin, and an increase in the content of

Table 2

Effect of SO_2 on the Pigments of Forage Grasses

So_2 Concentration	Time elapsed after action	Vulnerability, %	Amount of Pigments in 1 g of Green Weight, % of Control						Ratio $\frac{Xa}{Xb}$	Ratio $\frac{Xa+b}{y.\ p.}$	Ratio $\frac{X}{car.}$
			Chlorophyll a	Chlorophyll b	Carotene	Lutein	Violaxanthin	Neoxanthin			
Fescue - tillering											
$2{,}5\times10^{-5}$	1 hr.	0	98	108	56	94	64	69	$\frac{3{,}65}{3{,}34}$	$\frac{5.3}{6.9}$	$\frac{10{,}2}{14{,}4}$
5×10^{-5}	1 hr.	—	100	95	73	99	129	120	$\frac{4{,}3}{4{,}5}$	$\frac{5{,}0}{4.5}$	$\frac{12{,}1}{18{,}5}$
	24 hr.	13,8	109	126	155	130	192	232	$\frac{3{,}95}{3{,}4}$	$\frac{6{,}2}{4{,}25}$	$\frac{9.2}{9{,}6}$
10^{-4}	1 hr.		46	55	100	46	35	44	$\frac{4.9}{4{,}1}$	$\frac{4.7}{4.9}$	$\frac{24{,}7}{10{,}8}$
	24 hr.	37				88	57	75			
2×10^{-4}	1 hr.	—	114	110	108	88	89	111	$\frac{4{,}1}{4{,}25}$	$\frac{3{,}88}{4{,}6}$	$\frac{9{,}4}{8{,}1}$
	24 hr.	60	147	255	—	130	93	160	$\frac{6{,}0}{3{,}5}$	— —	— —
4×10^{-4}	1 hr.	—	81	81	—	99	81	81	$\frac{3{,}6}{3{,}6}$	4.9	7,3
	24 hr.	92	180	205	—	235	230	174	$\frac{3{,}5}{3{,}1}$	6,2	19,5
Timothy - tillering											
2×10^{-5}	1 hr.	0	59	58	—	92	105	112	$\frac{3{,}95}{4{,}0}$	$\frac{8{,}2}{4{,}8}$	7,8
5×10^{-5}	1 hr.	—	95	118	100	86	160	80	$\frac{5{,}65}{4{,}55}$	$\frac{4{,}7}{4{,}5}$	$\frac{8.2}{8{,}3}$
	24 hr.	41,1	83	76	—	105	106	82,5	$\frac{4{,}25}{4{,}7}$	5,1	11,0
10^{-4}	1 hr.	—	116	89,5	160	81.5	114	61	$\frac{3{,}35}{4{,}3}$	3.1 3.7	15,4 8,4
	24 hr.	55,6	—	—	208	116	124	102,5	—	—	$\frac{14{,}7}{8{,}0}$
2×10^{-4}	1 hr.	—	104	103	81	163	162	95,0	$\frac{4{,}4}{4{,}45}$	$\frac{5.3}{4{,}15}$	$\frac{15.5}{9.6}$

Table 2 (Cont'd)

Effect of SO_2 on the Pigments of Forage Grasses

SO_2 Concentration	Time elapsed after action	Vulnerability, %	Amount of Pigments in 1 g of Green Weight, % of Control: Chlorophyll a	Chlorophyll b	Carotene	Lutein	Violaxanthin	Neoxanthin	Ratio $\frac{Xa}{Xb}$	Ratio $\frac{Xa+b}{y.\ p.}$	Ratio $\frac{X}{xanz.}$
	24 hr.	90.7	86,5	230	0	100	87,5	96,0	$\frac{4,5}{1,7}$	—	14,0
4×10^{-4}	1 hr.	—	81.6	150	—	112	102	89	$\frac{7,4}{3,7}$	3.8	9,2
	24 hr.	93,0	123	228	—	140	81	130	$\frac{6,8}{3,6}$	4,6	13,5
					Timothy - booting						
5×10^{-5}	1 hr.	—	79	98	—	—	73	116	$\frac{3,95}{3,15}$	4,1	5,8
	24 hr.	58,3	60,6	119	—	60	56,5	96	$\frac{5,9}{3,25}$	— —	— —
10^{-4}	1 hr.	—	100	70	56	109	84	77	$\frac{3,0}{4,1}$	4.9 5,1	11,2 18,6
	24 hr.	82	64	58	—	—	134	—	$\frac{3,3}{3,6}$	5,3	28,5
2×10^{-4}	1 hr.	—	96	100	100	68	83,5	107	$\frac{4,4}{4,2}$	4,8 5,5	7,0 5.6
	24 hr.	56	75	65,5	—	59	73	70	$\frac{2,9}{3,3}$		
					Timothy - blooming						
2×10^{-5}	1 hr.	—	68	50	—	70	—	80	$\frac{4,16}{5,7}$	—	10,0
	24 hr.	82	108	100	—	95	93	72	$\frac{4,03}{4,4}$	5,6	13,2
5×10^{-5}	1 hr.	—	57,5	41	—	64	71,5	43	$\frac{5,6}{7,8}$	5,1	22.0
	24 hr.	100	42,2	67,5	—	36	27,4	44	$\frac{3,7}{2,4}$	3,6	14,3
10^{-4}	1 hr.	—	108	89	71,8	127	132	73,8	$\frac{4,0}{4,9}$	4,1 3,9	8,2 13,1
	24 hr.	100	56	89,5	—	79	96,5	150	$\frac{3.7}{2,3}$	4,2	11,6

Note. In the last three columns, the control is in the numerator and the experiment is in the denominator.

chlorophyll a, carotene, and violaxanthin. On the second day, an increase in the content of all the yellow pigments was observed. The 2 x 10^{-4} SO_2 concentration caused a decrease in the content of carotene and neoxanthin, and an increase in the content of the remaining pigments. In the timothy, on the second day, there was an increase in the content of chlorophyll b and a decrease in the content of the remaining pigments.

In the timothy, on the first day, the highest SO_2 concentration, 4 x 10^{-4}, caused a decrease in the content of chlorophyll a and neoxanthin. At the same time, an increase in the content of chlorophyll b and lutein was observed. On the second day, an increase in the content of all the pigments except carotene and violaxanthin was observed.

Thus, in contrast to the meadow fescue, low SO_2 concentrations cause more serious changes in the composition and ratio of the pigments in the timothy than high concentrations. Chlorophyll a and b are destroyed more extensively in the timothy by low SO_2 concentrations. High SO_2 concentrations have a stabilizing effect on chlorophyll. However, after the action of low SO_2 concentrations, 5 x 10^{-5}, the chlorophyll content continues to decrease on the second day, whereas its content increases after the action of high SO_2 concentrations (4 x 10^{-4}). In the timothy, in contrast to the meadow fescue, low SO_2 concentrations do not destroy the carotene on the first day, and act most destructively on the second day. The effect of high SO_2 concentrations on timothy and meadow fescue is similar. In the timothy, SO_2 has a lesser influence on xanthophylls than in the meadow fescue. At the same time, the increase in the content of xanthophylls on the second day after the action of SO_2 is more pronounced in the meadow fescue than in the timothy.

During the booting stage of the timothy, sulfur dioxide in the concentration of 5 x 10^{-5} destroys lutein completely, chlorophyll a partially, and chlorophyll b only slightly, and increases the content of neoxanthin. On the second day, a decrease is observed in the content of chlorophyll a, violaxanthin, and neoxanthin, and an increase in the content of chlorophyll b and lutein.

In the timothy, on the first day, sulfur dioxide in the concentration of 10^{-4} caused a decrease in the content of chlorophyll b, carotene, violaxanthin, and neoxanthin. On the second day, a decrease in the content of all the pigments except violaxanthin was observed.

In the timothy, sulfur dioxide in the concentration of 2 x 10^{-4} caused a stabilization of the content of chlorophyll a and b and carotene, and a decrease in the content of lutein and violaxanthin. On the second day, a decrease in the content of all the pigments was observed.

Thus, during the booting stage of the timothy (as during the tillering stage), chlorophyll, carotene, and lutein are more extensively destroyed by low SO_2 concentrations. The most stable of the yellow pigments during this stage is neoxanthin.

During the blooming stage of the timothy, low SO_2 concentrations, 2.5×10^{-5}, cause a more substantial destruction of chlorophylls a and b and yellow pigments. On the second day, an increase in the content of the pigments is observed.

The 5×10^{-5} SO_2 concentration causes a decrease in the content of all the pigments in the timothy on the first and second day. However, the content of chlorophyll b increased on the second day. In the timothy, the 10^{-4} SO_2 concentration caused a decrease in the content of chlorophyll b, carotene, and neoxanthin and an increase in the content of chlorophyll a, lutein and violaxanthin on the first day; on the second day, there was a decrease in the content of all the pigments except neoxanthin.

Thus, during the blooming stage of the timothy, the stability of chlorophylls and xanthophylls is similar. On the first day of the experiment, chlorophyll a is more resistant to the action of SO_2, but on the second day its resistance is lower than that of chlorophyll b.

Discussion

The two species of forage grasses which we studied, meadow fescue and timothy, show significant differences in gas resistance during the tillering stage. Under similar experimental conditions, the same SO_2 concentrations (with the exception of below-sublethal and above-lethal concentrations) cause a greater vulnerability in the timothy than in the meadow fescue. The character of the vulnerability curves of the plants as a function of SO_2 concentrations during the tillering stage is different: in the meadow fescue the relationship is more direct, proportional, and in the timothy, almost logarithmic. It should be noted that in the meadow fescue, the range of SO_2 concentrations between the sublethal and lethal doses is wider than in the timothy. This undoubtedly indicates a greater resistance of the meadow fescue to SO_2.

During the ontogeny of timothy, one observes in connection with an intensification of the vital processes, a decrease in resistance and hence, an increase in vulnerability in the presence of similar SO_2 concentrations. This reaffirms the dependence of the gas resistance of plants on the morphophysiological rhythms, on stages of growth and development, and on the intensity and direction of the physiological-biochemical processes in the leaves.

Despite the marked biological nature of the growth and development) and the physiological-biochemical (gas resistance) difference between the two plant species which we studied - meadow fescue and timothy - the pigment composition of the leaves during the tillering stage is very similar. It is possible that during other stages (booting, heading, blooming), differences in the pigment composition exist, but to find them it would be necessary to continue the studies with the meadow fescue during its second year of life. In the timothy, an increase in the concentration of the pigments is observed during ontogeny; this is important in connection with the intensification of the life processes in plants entering the reproductive stage.

It is possible that the revealed increase of pigment concentrations in the timothy is only seeming to be so as a result of a decrease in the strength of the bonding between the pigment and the protein-lipoid complex. If such be the case, then one of the causes of the increased vulnerability of the timothy during the booting and blooming stages becomes clear: the increase in the sensitivity of the pigments to SO_2 and light during the booting and blooming stages results from a decrease in the protective influence of proteins. This is associated with an increase in the extractability of the pigments.

At the same time, the ratio of the pigments in the timothy during the booting and blooming stages remains almost exactly the same as during the tillering stage. The stability of the ratio of the various pigments in the leaves during ontogeny appears to be a hereditary characteristic developed by evolution.

The effect of SO_2 on the pigment composition of the plants during the tillering stage varied in the plants studied. To some degree this can be related to the biology of the species and their differences in gas resistance. In the meadow fescue, a more direct proportional concentration dependence of the destruction of chlorophyll and vulnerability of the leaves is observed. In comparison with the timothy, in the fescue the xanthophylls are destroyed more extensively, and chlorophyll is comparatively more resistant to SO_2. The fescue displays more clearly its ability to increase the content of pigments in injured leaves. The mechanism of restoration of the pigments in injured leaves is unclear. Two explanations are possible: 1 - intensification of pigment synthesis and 2 - increase in the extractability of pigments under the influence of SO_2. The latter hypothesis is more plausible, since the greatest increase in the content of pigments was observed on the second day after the action of high SO_2 concentrations, which appear to cause something like a fixation of the plant tissues and a high vulnerability. In this case, there can be no question of the existence of complex processes of biosynthesis of pigments. More substantial differences in the change of the pigment composition of the leaves in the two species of forage grasses are observed in the effect of low SO_2 concentrations, i.e., concentrations closer to those acting on vegetation under industrial conditions.

There are some marked differences in the nature of the action of low and high SO_2 concentrations on the pigments of plants. For the most part, low SO_2 concentrations cause the destruction of many pigments even on the first and second day (timothy) or an increase in the content of pigments on the second day (meadow fescue). High SO_2 concentrations seem to stabilize (fix) the pigment composition. An increase in the content of the pigments (xanthophylls in timothy) is sometimes observed. In the meadow fescue, the increase in the content of pigments, with the exception of carotene, is more pronounced on the second day. This type of effect of SO_2 may be explained by differences in the chemistry of decomposition of the pigments. It may be postulated that low SO_2 concentrations cause an intensification of the enzymatic oxidation of pigments as a result of a slight acidification of the protoplasm and intensification of the activity of hydrolytic enzymes. High SO_2 concentrations cause a considerable acidification of the pH of the protoplasm, have an inactivating influence on hydrolytic enzymes, and promote a stabilization of the pigment composition. In this case, by destroying the protein-lipoid complex in the plastids, SO_2 simultaneously causes an increase in the extractability of the pigments, and thus the values of the pigment content which are obtained on the second day are too high.

During the booting and blooming stage of the timothy exposed to SO_2, no increase in the content of pigments is observed on the second day with the exception of the 5×10^{-5} concentration (booting) and 2.5×10^{-5} (blooming). This is obviously due to a change in the ontogenetic state of the plants. It is possible that such an influence of SO_2 on the pigments is also related to the low regenerating capacity of the cellular structures in chronologically old leaves. A further decomposition of the pigments at these stages on the second day in the case of exposure to high SO_2 concentrations probably takes place as a result of autolysis during the destruction of plastids.

Under the influence of SO_2, on the first and second day of the experiment, pheophytin bands were observed on the chromatograms in cases of decrease of the chlorophyll content. In both cases, the destruction of carotene and chlorophyll was due to oxidation processes induced by SO_2. This can be determined from the character and chemistry of the processes leading to the formation of pheophytin from chlorophyll.

Conclusions

1. The forage grasses meadow fescue and timothy, which differ in gas resistance, are also markedly different during the tillering stage from the standpoint of the nature of the changes in their vulnerability in relation to gas concentration. The fescue is characterized by an almost directly proportional dependence, and the timothy, by a logarithmic dependence.

2. During the ontogeny of the timothy, there is observed a regular decrease of the gas resistance and a decrease of the sublethal and lethal SO_2 concentrations as a result of intensification of the physiological-biochemical

processes with the onset of the reproductive stage.

3. Timothy shows during ontogeny a general increase in the concentration of the pigments without any appreciable change in their proportions. This may be due to an increase in the extractability of the pigments at the end of the vegetative period.

4. Under the influence of SO_2, certain differences in the destruction of individual pigment systems are observed in the plant species studied during their tillering stage. As compared to the fescue, xanthophylls in the timothy are destroyed more extensively, whereas the stability of chlorophyll is about the same. It may be assumed that the bonding between the pigments and the protein in the meadow fescue is stronger than in the timothy.

5. Low SO_2 concentrations apparently cause an intensification of the enzymatic oxidation of the pigments, whereas high SO_2 concentrations, by inactivating the enzymes, cause a stabilization of the content of the pigments.

6. During the stages of booting and blooming of the timothy, a lack of restoration of the content of pigments was observed on the second day after exposure to SO_2. This can be regarded as a confirmation of our views concerning the change in the ratio of pigment forms differing in stability (aggregate and monomeric forms) during ontogeny and under the influence of SO_2.

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